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# BIOTA OF FRESHWATER ECOSYSTEMS. IDENTIFICATION MANUAL NO. 5. THE FRESHWATER AMPHIPOD CRUSTACEANS (GAMMARIDAE) OF NORTH AMERICA

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The identification of amphipods is rather difficult, especially because accurate determinations often depend on the recognition of diagnostic character combinations and the study of the whole morphology of the animals. In order to facilitate the identification of genera and the determination of species, analytical keys with accompanying illustrations are presented. Of further assistance are ~~the inclusion of~~ distributional maps showing the ranges of many of the species. A brief synopsis of pertinent ecological information and the type locality for each species are also given. (EPA)

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# FOREWORD

"The Freshwater Amphipod Crustaceans (Gammaridae) of North America" is the fifth of a series of identification manuals for selected taxa of invertebrates occurring in freshwater systems. These documents, prepared by the Oceanography and Limnology Program, Smithsonian Institution for the Environmental Protection Agency, will contribute toward improving the quality of the data upon which environmental decisions are based.

Additional manuals will include, but not necessarily be limited to, freshwater representatives of the following groups: branchiuran crustaceans (*Argulus*), isopod crustaceans (Asellidae), decapod crayfish crustaceans (Astacidae), leeches (Hirudinea), polychaete worms (Polychaeta), freshwater planarians (Turbellaria), aquatic dryopoid beetles (Dryopoidea) and freshwater clams (Sphaeriacea).

ABSTRACT

The amphipod crustacean family Gammaridae is represented in the freshwaters of North America by eight genera and 81 described species; numerous other species are still undescribed. These eight genera, with the number of described North American freshwater species in parentheses, include: *Gammarus* (9), *Crangonyx* (18), *Synurella* (4), *Apocrangonyx* (6), *Stygonectes* (29), *Stygobromus* (10), *Bactrurus* (3), and *Allocrangonyx* (2). Ecologically, the freshwater gammarids are an important group of aquatic invertebrates, with species found in a variety of biotopes, including lakes, streams, ponds, swamps, springs, and subterranean waters.

The identification of amphipods is rather difficult, especially because accurate determinations often depend on the recognition of diagnostic character combinations and the study of the whole morphology of the animals. In order to facilitate the identification of genera and the determination of species, analytical keys with accompanying illustrations are presented. Of further assistance are the inclusion of distributional maps showing the ranges of many of the species. A brief synopsis of pertinent ecological information and the type locality for each species are also given.



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# SECTION I

## INTRODUCTION

The major purpose of this manual is to assist in the recognition and determination of the freshwater species of amphipod crustaceans of the family Gammaridae in North America north of Mexico and to provide some useful information on their distribution and ecology. Amphipods belong to the order Amphipoda of the class Crustacea. Amphipoda is further classified in the superorder Peracarida of the subclass Malacostraca and is subdivided into four suborders consisting of Gammaridea, Hyperiidea, Caprellidea, and Ingolfiellidea. The family Gammaridae is one of about 57 families contained within the suborder Gammaridea (see Barnard, 1958, for a list of the families). Caprellidea and Hyperiidea are exclusively marine groups while Gammaridea and Ingolfiellidea have representatives in freshwater. Ingolfiellids are unknown from North America, however, thus only the gammarideans are represented in the freshwater environment of the continent.

Amphipod crustaceans are one of the largest and most prominent groups of freshwater invertebrates. Five families, including Corophiidae, Haustoriidae, Hyalellidae (superfamily Talitroidea), Pontogeneiidae, and Gammaridae, are represented in the freshwaters of North America. The first four families are represented by only four genera and five species, however, and only two of these species (*Hyalella azteca* and *Pontoporeia affinis*) are strictly freshwater forms. In contrast, Gammaridae is represented by nine genera and numerous species; seven genera are exclusively freshwater and five of these are known only from subterranean habitats (Holsinger, 1967). The other two genera, *Gammarus* and *Anisogammarus*, occur in marine, brackish, and fresh waters, but *Anisogammarus* is found in freshwater only on a marginal basis (three species along the Pacific coast) and is primarily a brackish and marine group. Eight genera, including *Gammarus*, *Crangonyx*, *Synurella*, *Apocrangonyx*, *Stygonectes*, *Stygobromus*, *Bactrurus*, and *Allocrangonyx*, are considered in this manual.

Prior to the papers of Hubricht and Mackin (1940), Hubricht (1943), and Shoemaker (1940, 1942a, 1942b), very little detailed information was available on the freshwater amphipod fauna of North America. In comparison with Europe, where papers on freshwater amphipods have been published steadily since the 1800's, the extent and distribution of the North American fauna was very poorly known. Although a few significant papers on the group were published around the turn of the century (late 1800's and early 1900's) and in the 1930's, it wasn't until the 1940's that a concerted effort to describe the freshwater fauna was initiated. Since 1940, approximately 25 major taxonomic papers have been published, six of them as recently as 1970-71. References to most of the pertinent literature dealing with the group are found in the bibliography of this manual.

Currently, thanks largely to the proliferation of taxonomic and ecological studies in recent years, 81 valid freshwater species of Gammaridae are now described and at least 100 more are recognized but as yet undescribed. Descriptions of many of the undescribed forms are at the moment in various stages of preparation (see remarks throughout this manual). Within this taxonomic framework, it was possible to prepare what are hoped to be reliable analytical keys to the eight genera and most of the described species. Since the group is still imperfectly known and new data are rapidly accumulating on taxonomy, distribution, and ecology, the writer actively solicits comments and criticisms from workers in the field on the utility of these keys. Refinements can undoubtedly be made, especially after the keys are put to the test of active use. Revisions, incorporating both corrections and new information, will certainly be needed in the not too distant future.

With the exception of *Stygonectes*, keys to individual species in each genus are included. A key to the species groups of *Stygonectes* was prepared but a key to the individual species was not. Following the keys are annotated lists incorporating pertinent information of the geographic distribution and ecology of each species. Also included are range maps of all but three species of *Gammarus*, *Crangonyx*, *Synurella*, *Stygobromus*, and *Bactrurus*. Since maps showing the distribution of species of *Apocrangonyx*, *Allocrangonyx*, and *Stygonectes* were recently published (Holsinger, 1967, 1969a, 1969b, 1971), they were not repeated here.

The keys and annotated lists are based both on the taxonomic literature and the writer's examination of material. Leading up to the preparation of this manual, approximately 2700 collections of amphipods were examined. Whenever possible, data relative to ecology were also compiled and analyzed. While some of the distributional information is based on the published literature, a significant percentage of it is being published here for the first time. Species ranges on the distribution maps are shown by continuous shading where locality records were more or less geographically contiguous. Where large gaps or disjunctions occurred in the ranges, they are so noted.

The continuous collecting and study of freshwater amphipods will doubtless result in the extension of many of the plotted ranges. In some instances, however, a more critical examination and statistical evaluation of some of the species will lead to considerable refinement and closer circumscription of other ranges. Clearly, as shown in the annotated lists, a great deal remains to be learned about the ecology and other aspects of the biology of the species concerned. This is especially true of the subterranean forms, where detailed information is presently available on the life history of only two or three species.

## ECOLOGY

Very general notes on the ecology of each species are included in the annotated lists, therefore only a broad summary is necessary at this point. Freshwater amphipods occupy numerous niches within the realm of the aquatic environment. Although many observations are available on the broader adaptive zones filled by these animals, very little is known about species interactions, community roles, and niche separation. Recent studies by Culver (1970, 1971) on the relationship of amphipod species in the cave stream communities of southern West Virginia, however, are rapidly adding to our knowledge of this long neglected field. Similar studies have been made by Hynes (1955) on some British gammarids and by Clemens (1950) and Minckley and Cole (1963) on various species of *Gammarus*.

A number of works contain general discussions on the ecology of freshwater Gammaridae. A few of the recent papers treating the broader aspects of this subject are those by Pennak (1953), Bousfield (1958), and Holsinger (1967, 1969a). The European species have been treated more thoroughly and in greater detail (see for instance Ginet, 1960a, 1960b). In general, freshwater gammarids are cold-stenothermal, photonegative, and thigmotactic. The majority of species are found in smaller bodies of water. Few species inhabit large rivers or the open water of larger lakes; most species are associated with the substrate in one or another. Amphipods are often abundant in small streams, sloughs, swamps, ditches, ponds (temporary and permanent), drains, seeps, springs, and cave streams and pools. The greatest number of species (ca. 65-70 percent of the total North American amphipod fauna) inhabit subterranean habitats, where many forms have been described from caves, wells, seeps, outlets of drains, and sometimes springs. Undoubtedly the interstitial environment, which is still poorly known in North America outside of what has been learned mostly through the indirect investigations of biospeleologists, contains numerous species that have yet to be discovered.

Many of the cavernicolous species are not restricted to caves *per se* but are also found in other nearby groundwater habitats such as wells and seeps. Moreover, dispersal through the interstitial medium between caves is strongly indicated by the distributional patterns of many cavernicolous species (Holsinger, 1967, 1969a). Not all subterranean species are restricted to cave and karst areas but some are found exclusively in groundwater seeps, wells, drains, etc. outside of such areas. While showing the same morphological specializations as true cave forms (i.e., loss of eyes and pigment and sometimes attenuation of appendages), these species are, strictly speaking, phreatobites and not troglobites. Since some species are found in caves as well as related goundwater habitats, these ecological categories overlap to some extent and are often correctly used interchangeably. While many species are troglobites and/or phreatobites, other species, such as

*Gammarus minus*, *G. troglophilus*, *Crangonyx floridanus* and *C. forbesi*, occur in caves with regularity but are also as common in springs and show very little morphological change from one biotope to another.

Aside from morphological differences that are apparently closely correlated with different adaptive zones, there are striking differences in the reproductive biology and population control among species adapted to different biotopes. Many of the species which occupy surface ponds, swamps, sloughs, and ditches, such as species of *Synurella* and *Crangonyx* in particular, have abbreviated life spans of about one year, produce large numbers of small eggs, and have sharp seasonal reproductive peaks. In contrast, the subterranean and cold-water spring forms have longer life spans (especially the cave species), produce fewer and larger eggs, and either breed continuously at a very gradual rate or do not have sharp seasonal reproductive peaks.

The abundance of amphipods in a given habitat is quite variable. With some notable exception, the subterranean habitats are characterized by having very sparse faunas, while in contrast, certain epigean habitats (especially ponds, ditches, sloughs, and swamps in the spring of the year) may often contain tremendous numbers of animals. Even spring and spring-run populations are sometimes quite large. *Gammarus minus*, for example, is sometimes represented by thousands of animals per square meter in springs. In aquatic habitats in general, amphipods are usually found under gravels, dead leaves, grass, and other kinds of debris, or in masses of vegetation.

In mud-bottomed cave pools, amphipods are often observed "walking" or scuttling along on the bottom substrate. A number of the cave pool species have been observed to burrow into the mud or clay substrate, sometimes spending considerable time beneath the surface. In addition to receiving nutrients from the clay, these animals are apparently able to survive periods of drought by migrating deep within their burrows below the zone of saturation (Ginet, 1960a; Holsinger, unpublished data). Although observations are rare for this kind of behavior in epigean species, a similar means of survival is almost certainly used by those forms which inhabit temporary ponds that dry up during the summer months.

Much of the other information available on freshwater amphipod ecology, such as coloration, feeding, mating behavior, and development, has been usefully summarized by Pennak (1953) and will not be repeated here.

## COLLECTING AND PRESERVATION

The collecting of freshwater amphipods is relatively simple but varies somewhat from one kind of biotope to another. For species which occur in streams, lakes and larger bodies of water, a fine-meshed dipnet is useful, especially if swept through masses of aquatic vegetation or debris. For quantitative sampling, the Surber bottom sampler for streams and the Ekman dredge for lakes or ponds are recommended.

In small bodies of water, amphipods can usually be removed directly from the substrate, particles of debris or aquatic vegetation by forceps or small art brushes (camel's-hair brush). These animals can also sometimes be removed from masses of vegetation by rinsing or shaking over a container. Where amphipods are found swimming or walking in the open on the bottom of pools, they can be sucked up into a syringe, then passed into a tea strainer (fine mesh) and finally removed to a container with a small brush. Procedures for collecting subterranean amphipods were described in some detail by the writer in a recent paper (Holsinger, 1967).

Amphipods as well as most other small crustaceans are best preserved in 70 to 75 percent ethyl alcohol. Commercial rubbing alcohol (either ethyl or isopropyl) can be used in emergencies but is not recommended for permanent storage. Amphipods can be stored indefinitely in 70 percent ethyl alcohol, although crowding should be avoided. Because the integumentary pigments of amphipods are based on various carotenoid-protein complexes, even the most darkly pigmented specimens lose most of their coloration after a short time in alcohol. Therefore, if color patterns are important for identification, they should be recorded while the animals are still alive or immediately after preservation.

## IDENTIFICATION

The problems inherent in the specific determination of gammarid amphipods have been emphasized by Bousfield (1958), Holsinger (1967), and Cole (1970a). The major difficulties with making accurate identifications are the: (a) lack of systematic significance associated with the genitalia, (b) variation between size classes and successive instars, (c) pronounced sexual dimorphism in some species, (d) variation in size and proportion of a number of taxonomically important characters in older animals, and (e) overlapping ecology and geographic distribution of many species.

In contrast to some groups of crustaceans, where reliance on only a few morphological characters is necessary for the separation of closely related species, taxonomic discrimination of amphipod species frequently demands that much of the "whole morphology" of the animals be considered. Diagnostic character combinations are also useful, if not mandatory, in many instances. One of the most reliable means of separating morphologically closely related species is the use of the "yardstick of difference" derived from a knowledge of morphological differences between closely related sympatric or syntopic species.

For routine identification to generic level and often to specific level, specimens can be studied under a dissecting microscope without previous preparation of material. Watch glasses with black dissecting wax on the bottoms, small brushes, watchmaker's forceps, and fine needles are necessary for manipulation and dissection of amphipods.

For more refined study and often for the positive determination of species, the preparation of slide-mounted appendages and other external body parts is required. Temporary slide mounts can be made with glycerin. The advantage of using this method is that it allows the investigator a great deal of flexibility in manipulating appendages for observation in different planes. The disadvantage is that small appendages must be returned to a microvial for permanent storage and then removed and remounted for further study. The risk of losing one or more of these critical structures is compounded by each subsequent examination. Permanent slide mounts can be made with one of several commercially available mounting media, such as Hoyers, "Turtox CMC-10", and glycerin jelly. This method has the disadvantage of limiting flexibility of manipulation, but it has the advantage of bringing together in one place a permanent assemblage of appendages for continued reference. The adoption of a satisfactory method, however, should be left to the individual investigator, who, after some trial and error, will arrive at a technique that best suits his purpose. Further reference to equipment, techniques, and procedures which have been satisfactorily used in the study of amphipods and related crustacean groups are found in Pennak (1953) and Holsinger (1967).

## MORPHOLOGY

The illustration of a representative gammarid amphipod shown in Figure 1 has been prepared to facilitate the recognition of diagnostic morphological structures. The use of the keys will be made much easier if the reader is familiar with external morphology. Although many of the important morphological differences between genera and species have been illustrated piecemeal at different places in the keys, the necessity of having the proper perspective of how the "pieces" fit into the makeup of the whole animals should be emphasized.

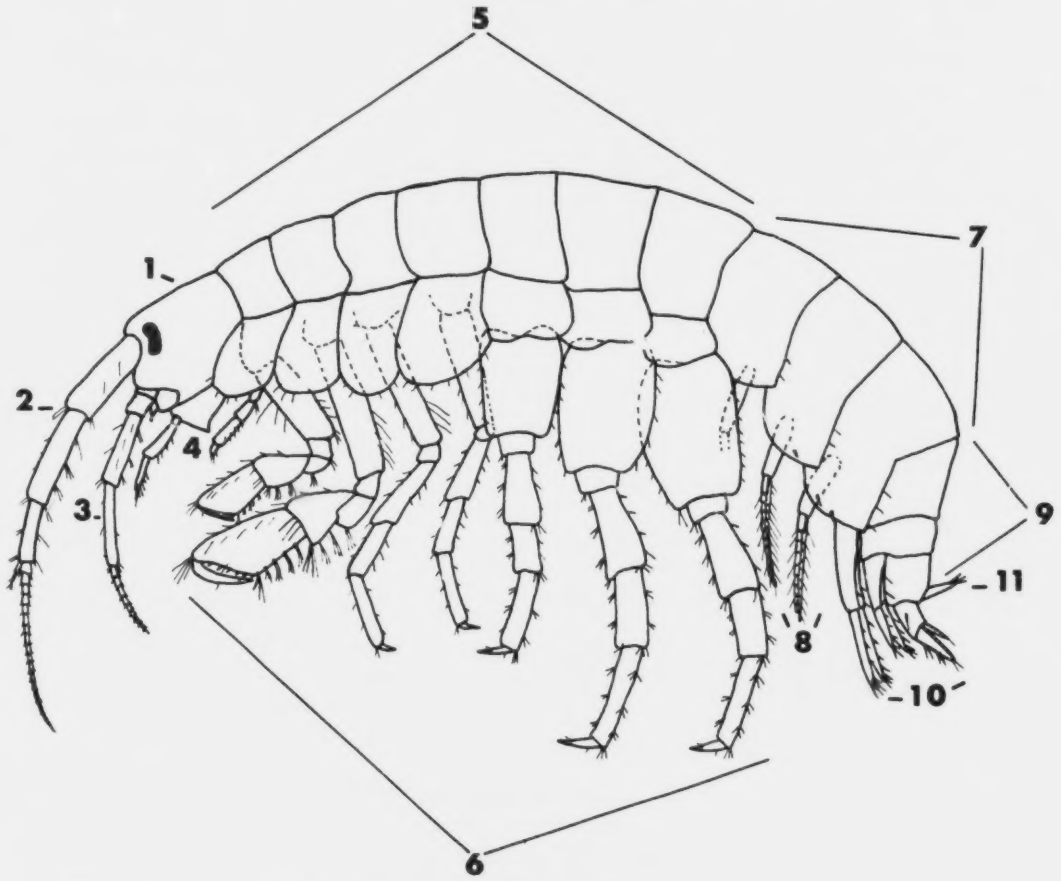


Figure 1.-- Generalized freshwater gammarid amphipod, showing principal external structures. 1, head; 2, antenna 1; 3, antenna 2; 4, mouth parts (shown in detail in Fig. 2); 5, pereonites 1-7; 6, pereopods 1-7 (including gnathopods 1 and 2); 7, pleonites 1-3; 8, pleopods 1-3; 9, uronites 1-3; 10, uropods 1-3; 11, telson.

In order to further familiarize the reader with the morphological structures used in the taxonomy of freshwater gammarid amphipods, each basic structure, beginning anteriorly, will be defined briefly. Since, in the past, morphological nomenclature has not always been consistent and different terms have been employed to designate the same appendage or external part, a standard usage has been adopted and applied consistently throughout the following keys. For comparison and further reference, the reader is referred to an excellent diagnosis of the morphological structures of the families of marine Gammaridea by Barnard (1969).

Head region: The head is composed of six completely fused segments (five head segments and the first thoracic segment) and bears one pair of sessile compound eyes. The latter are often greatly reduced or absent in the subterranean forms. The interantennal lobe is the small, variously rounded part of the head situated laterally on either side between the peduncles of the first and second antennae.

Antenna 1 (one pair): This appendage, sometimes called the antennule in other crustacean groups, consists of a three-segmented peduncle, followed by a multisegmented, primary flagellum. The accessory flagellum arises at the distal end of the third peduncular segment and has several tiny segments or articles. Small, linear-shaped calceoli are often found on many of the primary flagellar segments in the subterranean forms.

Antenna 2 (one pair): This appendage is made up of five unequal peduncular segments, followed by a multisegmented flagellum. The second antenna is typically shorter than the first antenna, and in *Crangonyx*, *Synurella*, and *Gammarus* it often bears conspicuous paddle-shaped sensory structures (calceoli) which are common in males but usually lacking in females.

Mouth parts: Six different structures make up the mouth parts as follows -- the upper lip, one pair of mandibles, two pairs of maxillae (maxilla 1 and 2), one pair of maxillipeds, and the lower lip.

Pereonites: These are the seven free thoracic segments of the body making up the pereon and bearing one pair of pereopods each. The first thoracic segment (not a pereonite) is fused with the head and bears the maxillipeds of the mouth parts.

Pereopods: Seven pairs of thoracic appendages including the first two pairs called gnathopods. The gnathopods differ from the other pereopods by being subchelate. Some workers number the gnathopods separately from the other pereopods, i.e., gnathopods 1 and 2 and pereopods 1-5. This writer, however, numbers the pereopods successively from 1 to 7 but refers to the first two pairs as gnathopods 1 and 2. The spelling of pereopod has been modified from other spellings, *viz.*, peraeopod or pereiopod. The seven segments or articles of the pereopods are referred to by number with the following exceptions: dactyl(s) for segment 7, propod(s) for segment 6, basis(es) for the expanded second segments of pereopods 5, 6, and 7, and coxa(e) for segment 1.

Brood plates: Four pairs of ventral plates or lamellae arise from inside and near the base of the first segment (coxa) of pereopods 2-5. These structures are characteristic of females and become fringed with setae at sexual maturity. They are sometimes called oostegites, marsupial plates, or brood lamellae. During the brooding of eggs, these plates become interlocked by their marginal setae to form the brood pouch.

Coxal plates: Seven pairs of lateral plates which are actually extensions of the coxae and which extend downward to cover the coxae and usually part of the bases.

Coxal gills: These are usually flattened, oblong to subovate structures, attached to the inside and near the base of the coxae and occur on pereonites 2-6 and sometimes on 7.

Sternal processes: These structures are usually present in species of the *Crangonyx* group but are absent in species of *Gammarus* and *Allocrangonyx*. Sternal processes are sometimes referred to as sternal gills but whether or not they function as accessary respiratory structures in all species is debatable. When present, sternal processes occur as follows: one, two, or three single, slender processes (often finger-like) on pereonites 2, 3, and 4; a single pair of slender processes on the first pleonite; and two pairs of laterally placed, simple or bifurcate processes (often sickle-shaped or lanceolate) on the ventral surface of pereonites 6 and 7.

Pleonites: The first three segments of the abdominal region containing laterally placed abdominal side plates (see below) and bearing one pair of pleopods each.

Abdominal side plates: These occur as paired, lateral plates or pleurites of the three pleonites and are fused to the body dorsally but are generally free posteriorly and ventrally. These structures are also called epimera (singular = epimeron).

Pleopods: Paired, biramous appendages borne by each of the three pleonites. Two or more small coupling spines (hooks) are found on the inside distal margin of the peduncles and are used for engaging the pairs of pleopods.

Uronites: The last three body segments of the abdominal region making up the urosome and sometimes called urosomites or urosome segments. These segments, along with pleonites 1-3, are sometimes referred to as the pleon or metasome. In *Gammarus* these segments are often humped mid-dorsally and bear small medial and lateral spines. In *Stygonectes*, *Apocrangonyx*, and one species of *Synurella* they are partially fused or coalesced.

Uropods: Three pairs of somewhat modified biramous appendages borne by the uronites and extending posteriorly, or in the case of the third,

semi-dorsally. Uropod 3 varies considerable intergenerically and is susceptible to radical modification. In the freshwater Gammaridae, uropod 3 varies from a biramous structure with two well developed rami in *Gammarus* to a greatly reduced structure that consists of only a peduncular remnant in some species of *Apocrangonyx*.

Telson: This flap-like structure is attached to the third uronite above the anus. It undergoes considerable change from genus to genus and varies from a deeply cleft, bilobed structure in *Gammarus* to a single flap with a complete apical margin in some species of *Stygonectes* and *Stygobromus*.

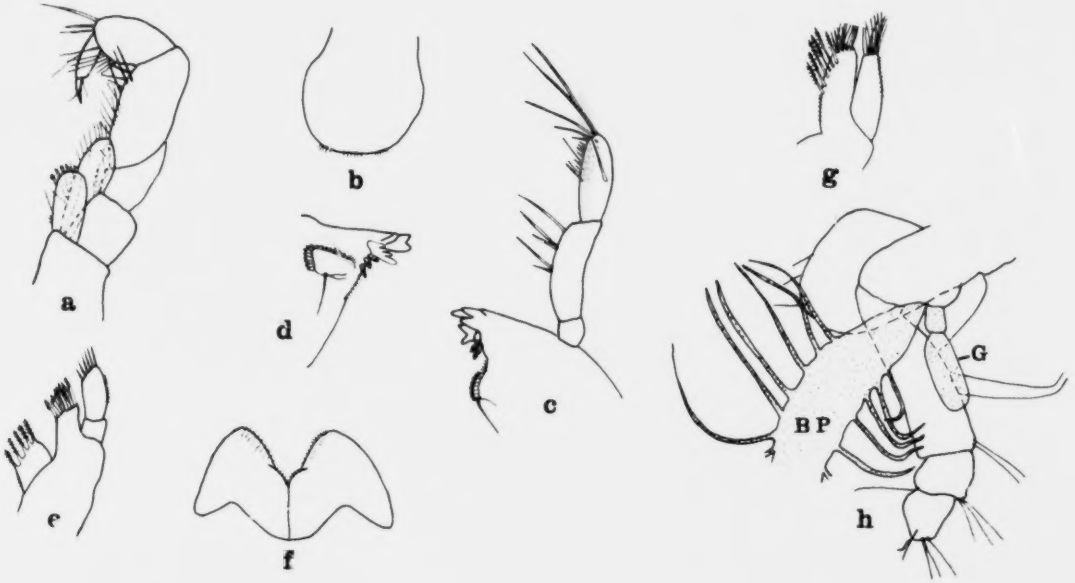


Figure 2. -- Structure of freshwater Gammaridae. Mouthparts of *Apocrangonyx* spp. (modified from Holsinger, 1969b): a, maxilliped; b, upper lip; c, right mandible; d, dentate part of left mandible; e, maxilla 1; f, lower lip; g, maxilla 2. *Apocrangonyx araeus*: h, gnathopod 2 (in part) showing attachment of brood plate (BP) and coxa gill (G).

## SECTION II

## FAMILY GAMMARIDAE

The family Gammaridae is the largest and most widespread member of the suborder Gammaridea and is represented by numerous genera (ca. 130) and species. Although the family is found in both marine and fresh water habitats, it is the only group of amphipods that has invaded continental freshwaters on such a broad, cosmopolitan basis. Many genera are exclusively freshwater (ca. 100) and some of these are exclusively subterranean (ca. 25).

During recent years amphipodologists have designated groups (sometimes called phyletic lineages) within the family. These groups reflect closely related genera or generic clusters rather than taxonomic categories in the strict sense. Some workers have suggested that some of these groups be elevated to subfamilial rank or, in some instances, to familial rank. Admittedly, the family is somewhat heterogeneous in composition and perhaps quite diverse in comparison with other families of the suborder. But it is the writer's opinion that these groups be retained, at least for the time being, as informal evolutionary catagories rather than be designated families or even subfamilies.

In North America (north of Mexico), three familial groups have been recognized. The eight genera of North American Gammaridae with freshwater species are arranged within these groups as follows: *Gammarus* group -- *Gammarus; Crangonyx* group -- *Crangonyx, Synurella, Apocrangonyx, Stygonectes, Stygobromus,* and *Bactrurus; Allocrangonyx* group -- *Allocrangonyx.*

Keys to the various families with freshwater species in North America have been published by Shoemaker (1942a) and Bousfield (1958). Without reference to these keys, however, Gammaridae is easily distinguished from other families by the following combination of characters (illustrated by Figs 1 and 2).

Body laterally compressed. Antenna 1 usually longer than antenna 2; accessory flagellum of antenna 1 with 2 to 7 small segments. Mandible usually with a palp (present in all North American genera north of Mexico); maxilla 1 with 2-segmented palp. Gnathopods subchelate; pereopods 5, 6, and 7 alike in structure but different in length; pereopod 7 about equal to pereopod 6 in length but often a little longer or a little shorter. Uropod 3 with or without rami, but outer ramus usually present although often greatly reduced; outer ramus longer than inner ramus when both rami are present. Telson entire or variously cleft.

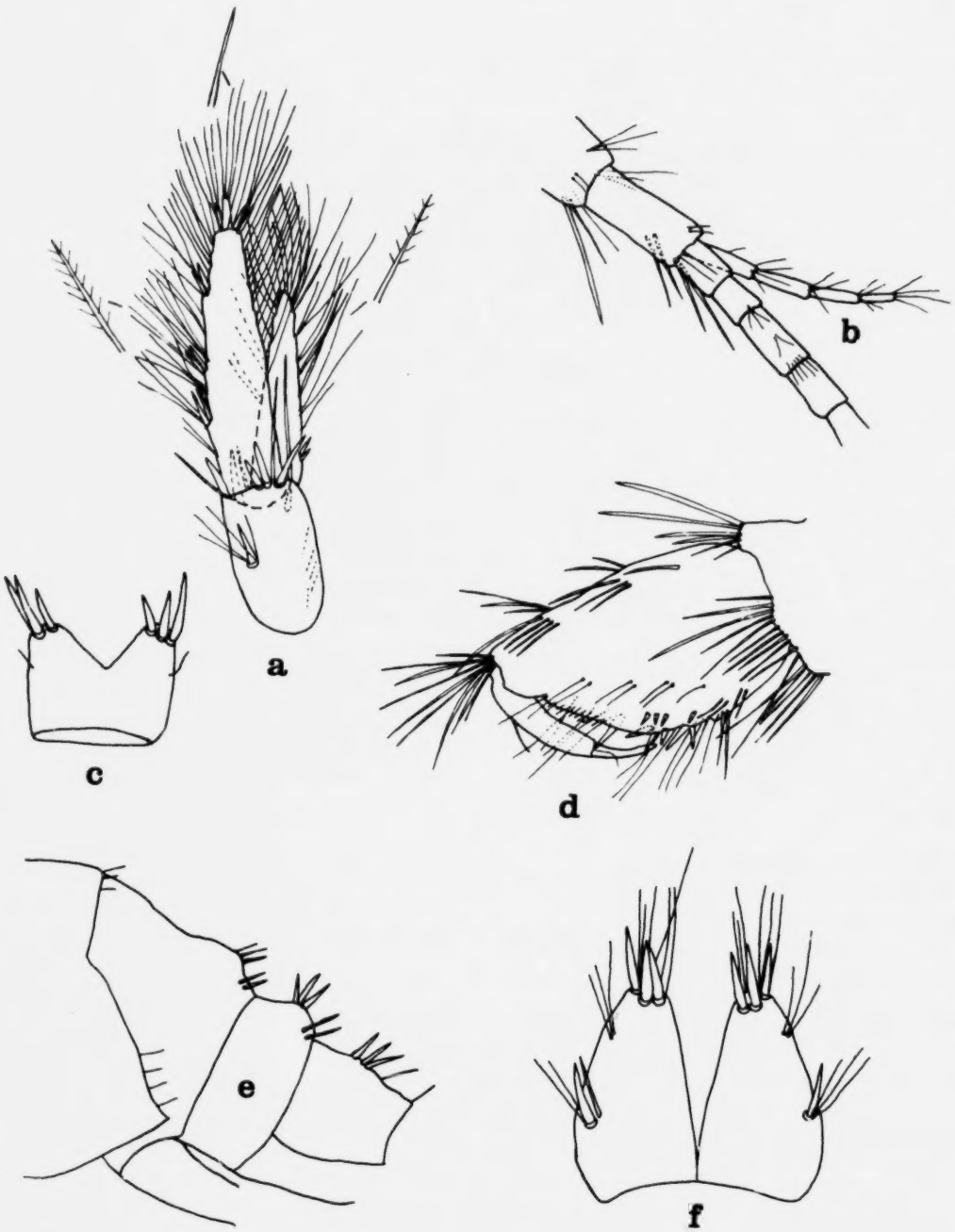


Figure 3. -- Structure of freshwater Gammaridae: a, uropod 3 of *Gammarus minus;* b, accessory flagellum of *G. minus;* c, telson of *Crangonyx antennatus;* d, gnathopodal propod of *G. minus;* e, uronites of *Gammarus acherondytes* (based on Bousfield, 1958); f, telson of *G. minus.*

## Key to Genera of the Family Gammaridae in North America

1 Accessory flagellum of antenna 1 with 2 to 7 segments (usually 3 or more)(Fig. 3b); gnathopodal propod palmar margins without distally notched spine teeth in either sex (Fig. 3d); uronites with prominent dorsal spines (Fig. 3e); uropod 3 biramous (Fig. 3a), rami well developed; telson cleft nearly to base (Fig. 3f): *Gammarus* (p. 17)

Accessory flagellum of antenna 1 with never more than 2 segments; gnathopodal propod palmar margins with distally notched spine teeth in males and usually in females (Fig. 4l); uronites without prominent dorsal spines; uropod 3, inner ramus reduced to a small scale or absent; telson cleft or not, if cleft then no more then 3/4 way to base (Fig. 3c) .... 2

2(1) Outer plate of maxilla 1 with 9 apical spines (Fig. 4d); dactyls of pereopods 6 and 7 with ventral spines (Fig. 4c); sternal processes absent; uronite 2 with 1 pair of very small dorsolateral spines; uropod 3 biramous, outer ramus elongate and 2-segmented: *Allocrangonyx* (p. 77)

Outer plate of maxilla 1 with 7 apical pectinate spines (Fig. 2e); dactyls of pereopods 6 and 7 without ventral spines; sternal processes usually present (Fig. 4a,b); uronite 2 without spines; uropod 3 biramous or uniramous, outer ramus not elongate but reduced to 1 segment or vestigial or absent (Fig. 4e,f,g) ..... 3

3(2) Antenna 2 of mature male with paddle-shaped calceoli (Fig. 4h); eyes usually present and pigmented; gnathopodal propod 2 usually larger than 1; pereopod 6 longer than 7; apical margin of telson distinctly cleft (Fig. 3c) ..... 4

Antenna 2 of mature male without paddle-shaped calceoli; eyes never present (of subterranean facies); gnathopodal propod 2 smaller, equal to, or larger than, 1; pereopod 7 sometimes longer than 6; apical margin of telson entire or with a shallow cleft (Fig. 4i) ..... 5

4(3) Dactyls of pereopods 5, 6, and 7 with 4 to 5 stiff setae or small spines on inner margins (Fig. 4j); uronites fused or not; outer ramus of uropod 2 of mature male normal (not deflected or curled); uropod 3 uniramous, outer ramus not exceeding length of peduncle (Fig. 4k): *Synurella* (p. 49)

Dactyls of pereopods 5, 6, and 7 with typically 1 stiff seta on inner margins (Fig. 5a)(excepting *Crangonyx setodactylus* which has 2 to 3 such setae); uronites not fused (Fig. 1); outer ramus of uropod 2 of mature male curled or deflected laterally (Fig. 5b); uropod 3 biramous, outer ramus longer than peduncle, inner ramus vestigial (Fig. 5d): *Crangonyx* (p. 29)

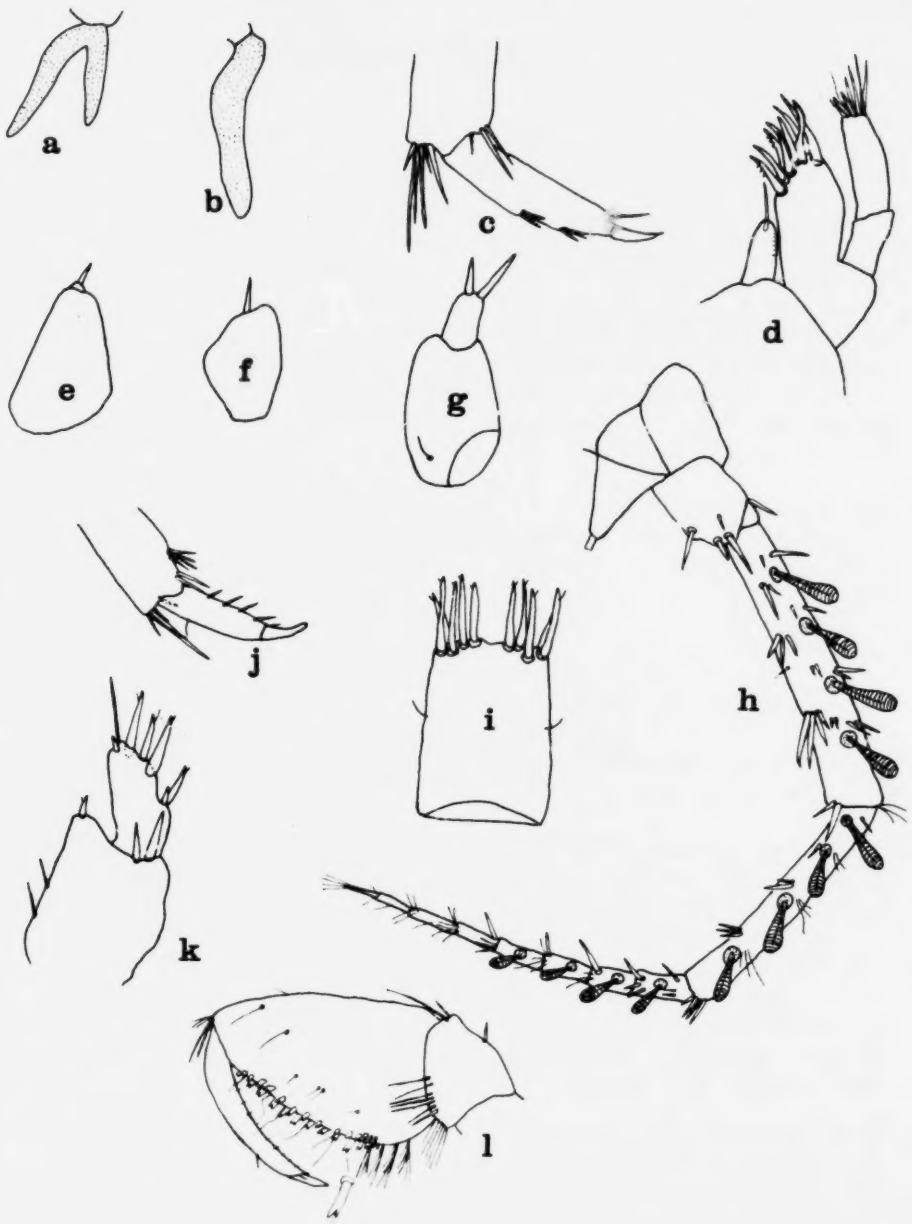


Figure 4. -- Structure of freshwater Gammaridae: a, bifurcate lateral sternal process of *Apocrangonyx araeus;* b, simple lateral sternal process of *Crangonyx packardi;* c, dactyl of pereopod 7 of *Allocrangonyx pellucidus;* d, maxilla 1 of *A. pellucidus;* e, uropod 3 of *A. araeus;* f, uropod 3 of *Apocrangonyx parvus;* g, uropod 3 of *Stygonectes alabamensis;* h, male antenna 2 (showing calceoli) of *Crangonyx antennatus;* i, telson of *Stygonectes emarginatus;* j, 7th pereopod dactyl of *Synurella dentata;* k, uropod 3 of *S. dentata;* l, 1st gnathopodal propod of *Stygonectes allegheniensis.*

5(3) Outer lobe of maxilliped with a row of small, blade-like spines on inner margin (Fig. 5e); pereopod 7 longer than 6; lateral sternal processes simple, not bifurcate; uropod 1 of mature male without distal peduncular process; uropod 3 biramous, inner ramus vestigial; outer ramus about as long as peduncle (Fig. 5f): *Bactrurus* (p. 73)

Outer lobe of maxilliped with stiff setae only on inner margin (Fig. 2a); pereopod 7 longer, equal to, or shorter than 6; lateral sternal processes bifurcate or not (Fig. 4a); uropod 1 of mature male often with distal peduncular process (Fig. 5c); uropod 3 uniramous, outer ramus shorter than peduncle and occasionally absent (Fig. 4e,f,g) ..... 6

6(5) Gnathopodal propod 2 about equal to or usually larger than 1; pereopod 6 usually longer than 7; lateral processes simple, not bifurcate (with exception of 1 undescribed species); uronites not fused: *Stygobromus** (p. 65)

Gnathopodal propod 1 often larger, but sometimes equal to or smaller than 2; pereopod 7 longer than 6; lateral sternal processes usually bifurcate (with a number of exceptions); uronites fused or nearly so ..... 7

7(6) Gnathopodal propod 2 equal to or larger than 1; outer ramus of uropod 3 vestigial or absent (Fig. 4e,f); size range of adults 2.0 to 7.0 mm: *Apocrangonyx** (p. 52)

Gnathopodal propod 1 usually larger than 2; outer ramus of uropod 3 small but neither vestigial nor absent; size range of adults, 4.5 to 20.0 mm: *Stygonectes** (p. 55)

* These three genera are often difficult to key out because a number of characters overlap in certain species. With one or two exceptions, however, *Stygobromus* and *Stygonectes* are easily separated on the basis of diagnostic character combinations. In comparison, *Apocrangonyx* is less distinct and there is some question as to whether this genus as presently defined is a natural group or an artificial one (see Holsinger, 1969a, 1969b, and below for further comments on this problem).

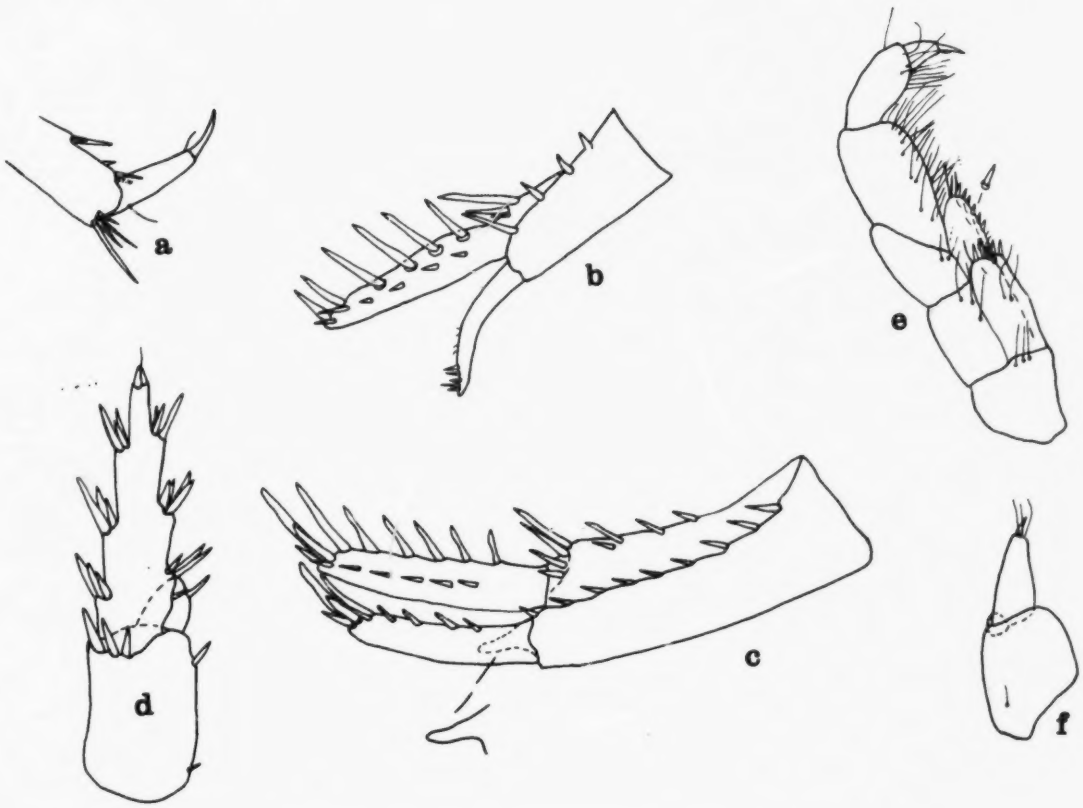


Figure 5. -- Structure of freshwater Gammaridae: a, dactyl of pereopod 7 of *Crangonyx antennatus;* b, male uropod 2 of *C. antennatus;* c, male uropod 1 of *Stygonectes indentatus;* d, uropod 3 of *Crangonyx forbesi;* e, maxilliped of *Bactrurus mucronatus;* f, uropod 3 of *B. mucronatus.*

## *GAMMARUS* Group

### Genus *Gammarus* (in part) Fabricius, 1775

The genus *Gammarus* (s. lat.), as presently understood, is composed of a number of subgenera and numerous species widely distributed throughout the Northern Hemisphere. Species occur in shallow marine, brackish, and freshwater habitats, but the largest number of species inhabit littoral brackish and fresh water biotopes. Considerable taxonomic confusion still exists within the genus, and as implied by Bousfield (1969) and Stock (1967), a world revision would be both desirable and necessary for a complete understanding of the systematics of this complex group. The current situation is further complicated by the presence of sibling species, sympatric ranges, overlapping ecology, extreme morphological variation, etc., especially among the brackish water forms. This confusion seems less pronounced, however, among the strictly freshwater species of the genus, where, despite overlapping ranges and several as yet unresolved species complexes, most species appear to be more clearly differentiated. Nevertheless, this may be an oversimplification of the true picture, especially in parts of the world where freshwater species of *Gammarus* have not yet been carefully studied.

Nine species are currently recognized from North American freshwaters. A number of other species have been described but are now regarded as synonyms (including *G. elki* which is considered a synonym of *G. minus* by this writer, as pointed out below). Two other species, *G. tigrinus* and *G. duebeni*, occur in brackish waters of the Atlantic coastal region but are occasionally found in marginal freshwater habitats. Only the strictly freshwater species (including *G. fasciatus* which may ocasionally occur in marginal brackish waters) are included in this manual. Recent papers by Bousfield (1958, 1969) treat some of the brackish water species (such as *G. duebeni*, *G. tigrinus*, *G. palustris*, and *G. daiberi*) and the reader is referred to these papers for additional information.

The past use of the subgenus *Rivulogammarus* to include some of the North American freshwater species (viz., *G. minus*, *G. troglophilus*, *G. pseudolimnaeus*, *G. bousfieldi*, etc.) by Shoemaker (1940), Bousfield (1958), Cole and Minckley (1961), and Holsinger (1969a) should be discouraged. Stock (1969) has recently given valid reasons for rejecting this name. Any further assignment of freshwater species of *Gammarus* to various subgenera should logically await a much needed revision of the genus on a world-wide basis (see above).

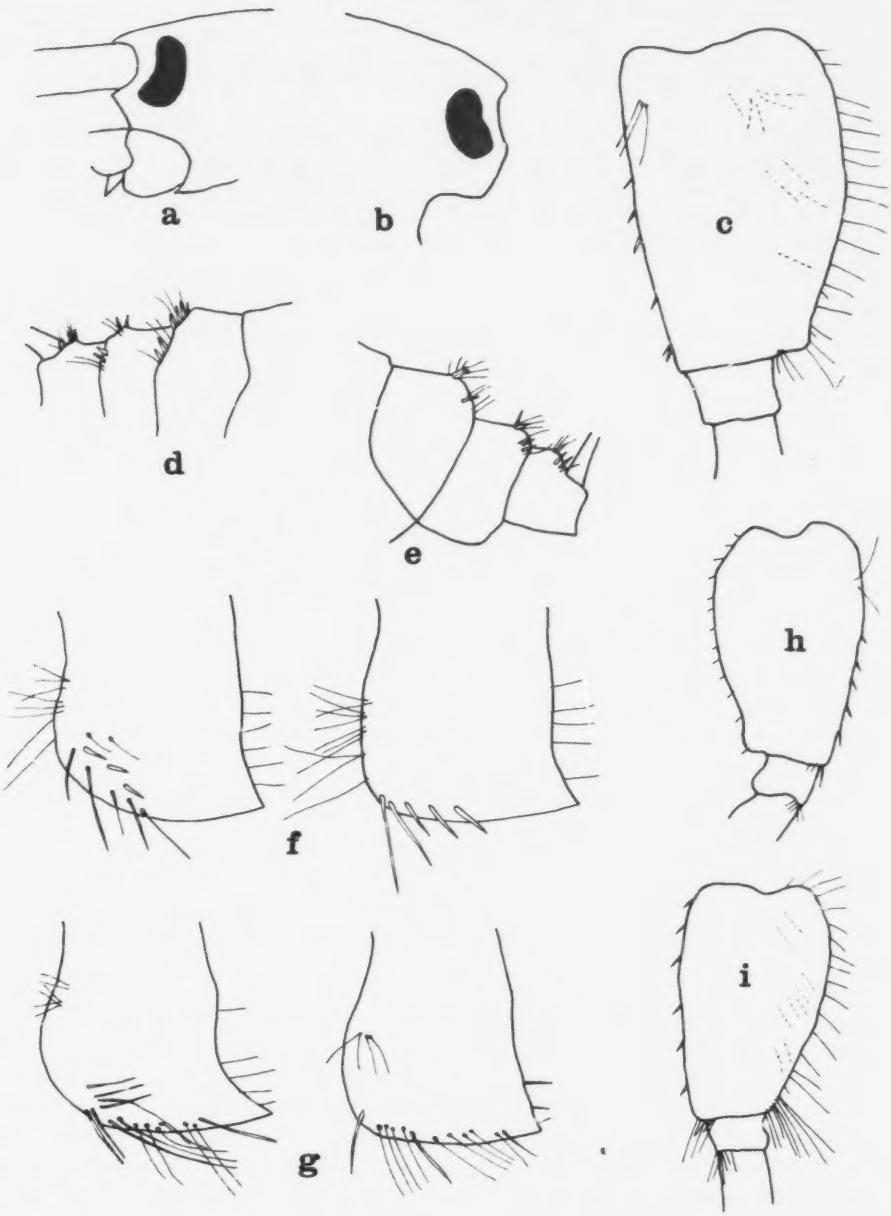


Figure 6. -- Structure of *Gammarus*: a, head (showing interantennal lobe) of *G. fasciatus* (based on Bousfield, 1958); b, head of *G. minus* (based on Holsinger and Culver, 1970); c, 7th pereopod basis of *G. troglophilus* (based on Bousfield, 1958); d, uronites of *G. bousfieldi* (based on Cole and Minckley, 1961); e, uronites of *G. pecos* (based on Cole and Bousfield, 1970); f, abdominal side plates 2 and 3 of *G. pecos* (based on Cole, 1970a); g, abdominal side plates 2 and 3 of *G. bousfieldi* (based on Cole, 1970a); h, 7th pereopod basis of *G. minus;* i, 7th pereopod basis of *G. fasciatus*.

## Key to the North American Freshwater Species of *Gammarus*

1 Antenna 2 richly setose; pereopod 7, distoposterior margin of basis not forming a free lobe but fusing directly (or nearly so) to segment proper, junction marked by a cluster of long setae (Fig. 6i)..... 2

Antenna 2 not richly setose; pereopod 7, distoposterior margin forming a free lobe, junction not marked by a cluster of long setae (Figs 6c,h) (although a few short ones may be present). ..... 4

2(1) Interantennal lobe of head, upper angle acute (Fig. 6a); antenna 2 about as long or often longer than antenna 1; palmar margins of male gnathopodal propods slightly concave: *G. fasciatus*

Interantennal lobe, upper angle rounded (Fig. 6b); antenna 2 shorter than antenna 1; palmar margins of male gnathopodal propods concave (but not strongly)..... 3

3(2) Male antenna 2 with calceoli; coxal plates 1 and 2, distoanterior margins with 1-2 short setae; ventral margins of abdominal side plates 2 and 3 not spinose (Fig. 6g); uronites dorsally humped (Fig. 6d): *G. bousfieldi*

Male antenna 2 without calceoli; coxal plates 1 and 2, distoanterior margins with 4 to 7 setae; ventral margins of abdominal side plates 2 and 3 spinose (Fig. 6f); uronites not dorsally humped (Fig. 6e): *G. pecos*

4(1) Posterior margin of basis of pereopod 7 with long setae (Figs. 6c, 7c)..... 5

Posterior margin of basis of pereopod 7 with short setae (Fig. 6h) ..... 6

5(4) Antenna 2 of both sexes with calceoli; palmar margin of second gnathopodal propod of male not concave; segments 4-6 of pereopods 5-7 with numerous long setae among spine clusters; pereopod 7, posterior margin of basis narrowing evenly to distal hind lobe (Fig. 6c): *G. troglophilus*

Antenna 2 of female without calceoli; palmar margin of second gnathopodal propod of male concave; segments 4-6 of pereopods 5-7 nearly devoid of long setae among spine clusters; pereopod 7, posterior margin of basis becoming concave distally (Fig. 7c): *G. pseudolimnaeus*

6(4) Interantennal lobe sharply angled above; antenna 2 without calceoli; uronites partially humped dorsally, with 20 to 22 rather prominent dorsal spines: *G. acherondytes*

Interantennal lobe rounded above; antenna 2 usually calceolate in male; uronites not humped (or not appreciably so) dorsally, with 10 to 18 rather small dorsal spines..... 7

7(6) Distoposterior corners of abdominal side plates 2 and 3 weakly acuminate, not produced (Fig. 7b); second segment of outer ramus of uropod 3 without plumose setae: *G. minus* (s. lat.)
This choice will also lead to *G. breviramus*, a recently described species that differs only in a few subtle ways from *G. minus* (see remarks below).

Distoposterior corners of abdominal side plates 2 and 3 strongly acuminate, produced (Fig. 7a); second segment of outer ramus of uropod 3 with plumose setae:
*G. lacustris* (s. lat.)

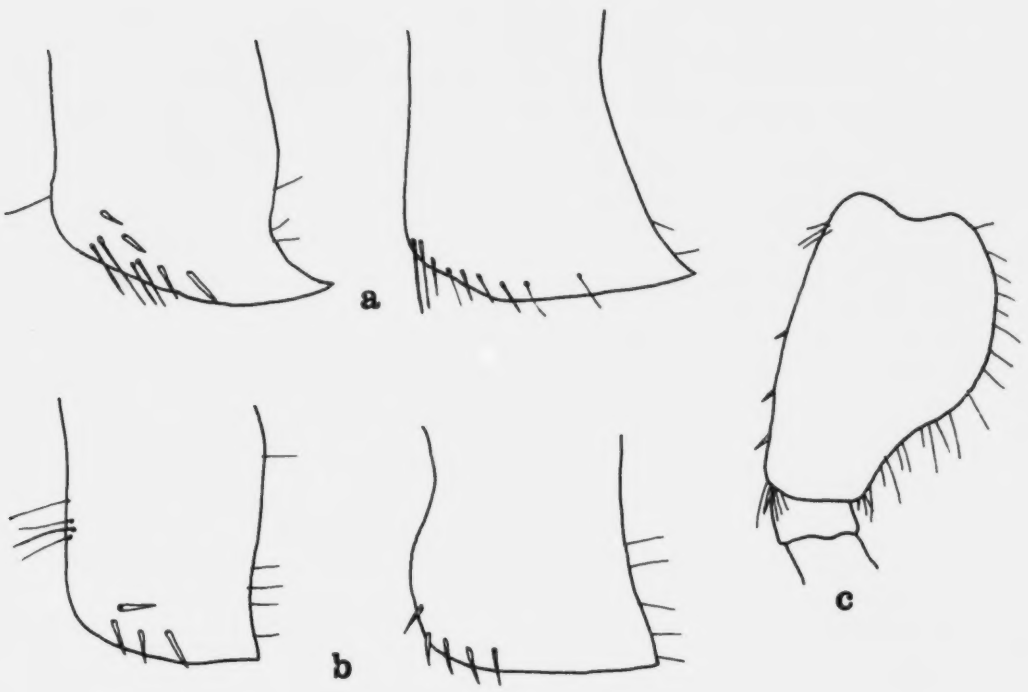


Figure 7. -- Structure of *Gammarus*: a, abdominal side plates 2 and 3 of *G. lacustris* (based on Cole, 1970a); b, abdominal side plates 2 and 3 of *G. minus* (based on Cole, 1970a); c, 7th pereopod basis of *G. pseudolimnaeus*.

## Annotated List of the Species

1. *Gammarus acherondytes* Hubricht and Mackin, 1940
Type Locality: Morrisons Cave, Monroe Co., Illinois.
This somewhat rare species is known only from four caves in Monroe Co., Illinois and one cave in St. Clair Co., Illinois (Fig. 8). It usually occurs syntopically with *G. troglophilus* but is much less common than the latter. Sexually mature males, up to 20.0 mm; sexually mature females, 12.0 to 16.0 mm. Clutch size up to 21 eggs (or more?). Very little is known about the life cycle of this species except that ovigerous females have been observed in summer and fall. The species usually inhabits small cave streams.

2. *Gammarus bousfieldi* Cole and Minckley, 1961
Type Locality: Doe Run, Meade Co., Kentucky.
This is a very distinct species, especially when compared with *G. minus*, with which it is often associated. *G. bousfieldi* is known only from two streams in northern Kentucky, the type locality and Fern Creek in Jefferson County (Fig. 8). Sexually mature males, 12.0 to 16.0 mm; sexually mature females are smaller. Although very little is known about the life cycle of this species, some important observations on its ecology and behavior were noted by Cole and Minckley (1961).

3. *Gammarus breviramus* Bousfield and Elwood, 1971
Type Locality: Small spring-fed stream, west fork of Walker Branch, 3 miles south of Oak Ridge, Anderson Co., Tennessee.
Since this species was only recently described the writer has not had time to examine the type material. However, on the basis of the description by Bousfield and Elwood (1971) it would appear to be very closely related to, if not nearly identical to, *G. minus*, with which it occurs sympatrically. The only differences discernible to this writer were the proportionately shorter uropods 1 and 2 in the male and possibly the proportionately longer inner ramus of the third uropod. These differences are subtle at best and are not made clear in the figures given in the description by Bousfield and Elwood (1971). A brief discussion of the ecology of this species can be found in Bousfield and Elwood (1971). *G. breviramus* is known only from the vicinity of its type locality (i.e., Walker Branch Watershed streams) where it is less common than *G. minus*.

4. *Gammarus fasciatus* Say, 1818
Type Locality: Probably a river in eastern Pennsylvania, the details of which are lacking in the original description.
This widely distributed species ranges from the upper Mississippi River drainage eastward throughout the Great Lakes area and south along the Atlantic Coastal plain to southern North Carolina (Fig. 8). Although primarily an inhabitant of lakes and rivers (see Bousfield, 1958), this species also occurs in small streams and occasionally in spring runs, especially in the southern part of its range. Sexually mature males, up to 14.0 mm; sexually mature females, 8.0 to 12.0 mm. Bousfield's 1958 comments on the life history of this species hold true in general, except that ovigerous females have been observed from February to April in the more southern parts of the range.

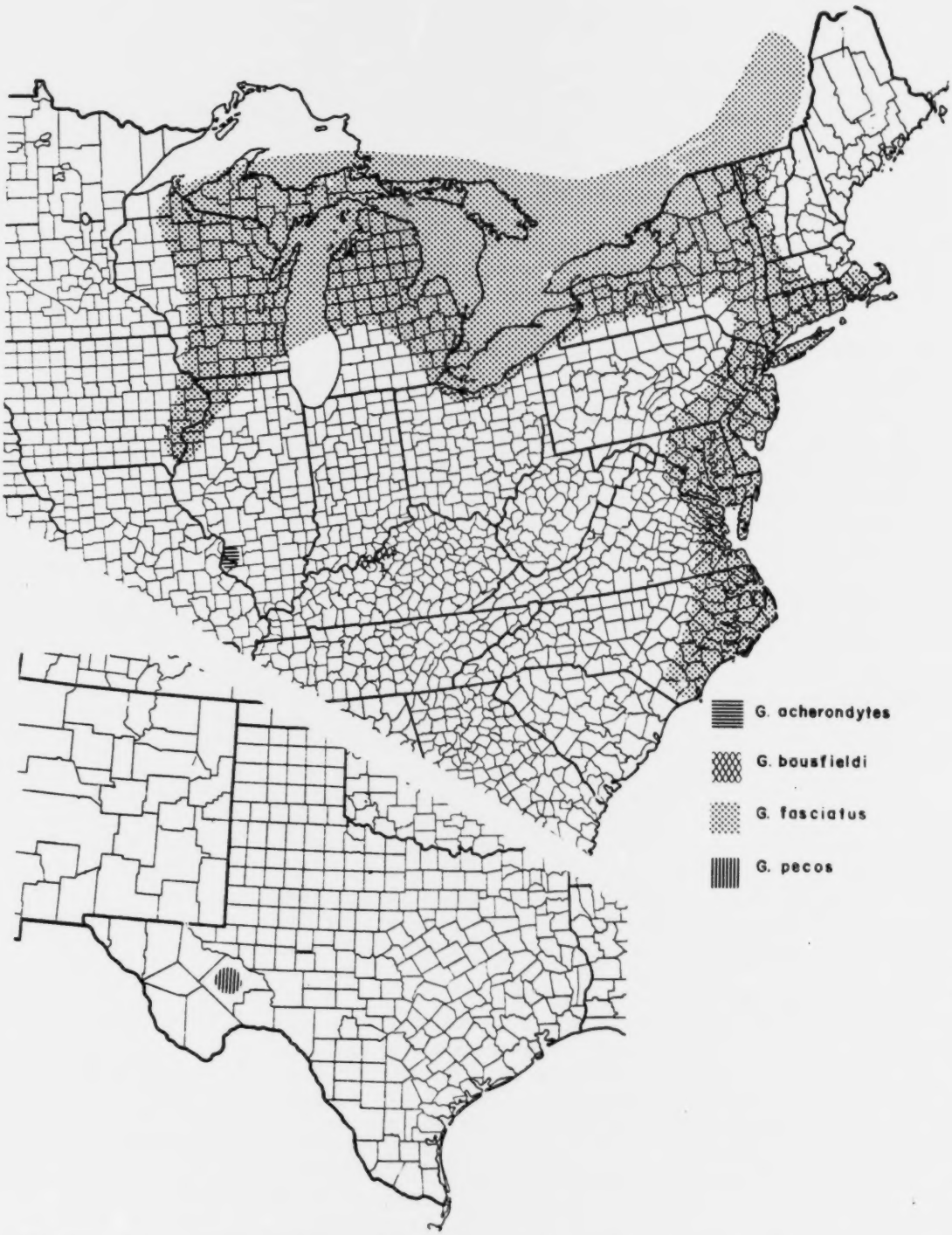


Figure 8. -- Distribution of species of *Gammarus* in North America.

As pointed out by Bousfield (1958), this species has been confused with at least two and possibly three other species of *Gammarus* in the past. Where the range of *G. fasciatus* overlaps or is contiguous with that of *G. tigrinus* in coastal areas of the eastern United States, the two species can be distinguished by differences in the setation and spination of the abdominal side plates (Cole, 1970a). Additional differences are also given in a key by Bousfield (1969). In the coastal areas extending from South Carolina westward to Louisiana, *G. fasciatus* is replaced by a complex of two to three closely related species which has characters in common with both *G. fasciatus* and *G. tigrinus*. Hubricht's records for *G. fasciatus* from South Carolina and Florida (Hubricht, 1943) are referrable to this complex, as well as a number of collections (unpublished data) from Louisiana and Mississippi currently in the United States National Museum of Natural History.

5. *Gammarus lacustris* s. lat.
Two subspecies were recognized by Bousfield as follows:
a) *Gammarus lacustris lacustris* G.O. Sars, 1864.
Type Locality: Northwestern Europe (specific location unknown).
b) *Gammarus l. limnaeus* S.I. Smith, 1874
Type Locality: Lake Superior, Ontario, Canada.
During the preparation of this manual, the writer studied numerous collections of *G. lacustris* s. lat. from localities in the northern and western United States, Canada, and Alaska in an attempt to more clearly delimit the ranges of the two subspecies recognized by Bousfield (1958). The diagnostic characters used to differentiate these two races, however, were found to be highly variable and without regional consistency. For example, some mature specimens from the western United States (within the range of *G. l. lacustris*) had as many as 18 dorsal spines on the uronites (range, 10 to 18), sub-reniform eyes, and as many plumose setae on the second segment of the outer ramus of the third uropod as that given for the eastern subspecies *G. l. limnaeus*. Furthermore, some specimens studied from well within the range of *G. l. limnaeus* had subrotund eyes and as few as 10 dorsal spines on the uronites. Moreover, in a recent study by Cole (1970a) on the epimera (abdominal side plates) of North American freshwater species of *Gammarus*, clear-cut differences in the shape, armature, and setation of these structures were not demonstrated for these two subspecies. Finally, with the exception of the disjunct populations in Oklahoma, the range of *G. lacustris* s. lat. appears to be continuous across North America, and separation into regionally allopatric populations seems unlikely. In all fairness, however, this problem is still far from being solved, and a search for genetic differences (as opposed to morphological ones) might be in order. Along these lines, H.B.N. Hynes of the University of Waterloo has attempted to cross breed members of the two subspecies but so has received inconclusive results (Bousfield, *in litt.*).

*G. lacustris* s. lat. is found throughout most of the western United States (especially in the cold alpine lakes of the Rocky Mountain region), across the northern part of the United States through the Great Lakes area, throughout most of Canada and Alaska north to the Arctic

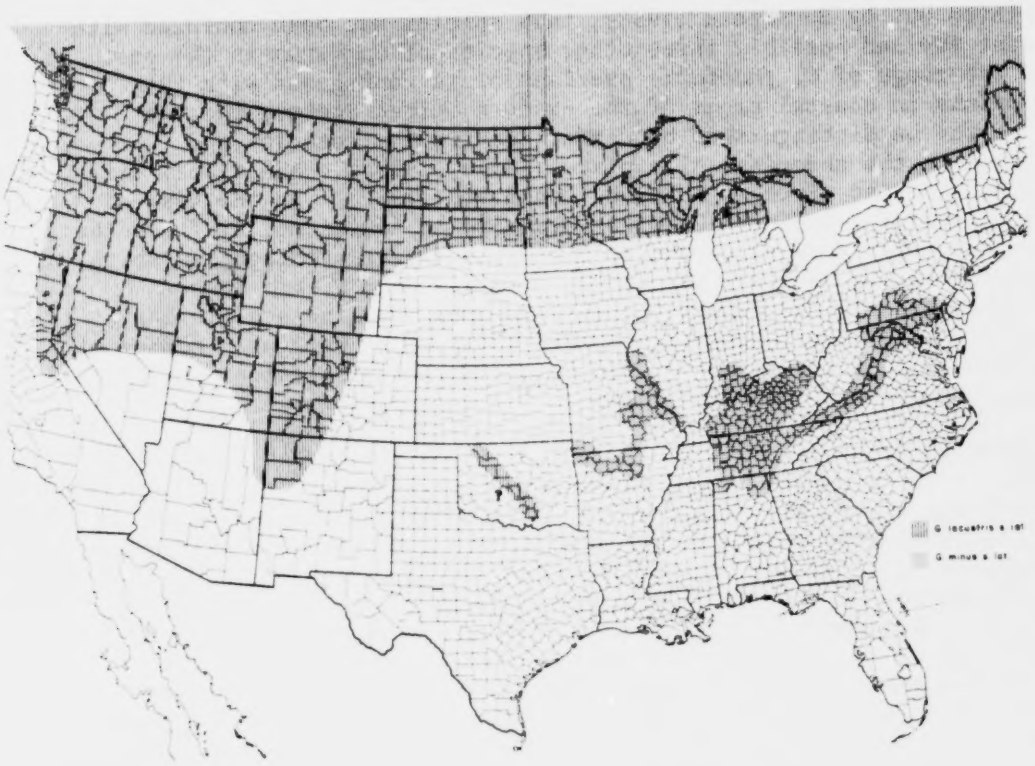

Figure 9. -- Distribution of species of *Gammarus* in North America. The complete range of *G. lacustris* is not shown; it extends throughout most of Canada and Alaska, north to the Arctic Circle and to Latitude 70° in some areas.

circle and latitude 70° in some areas (Fig. 9). The species is also found in northwestern Europe and disjunct populations occur in central Oklahoma. This species occupies a variety of cold-water habitats, including lakes, tundra ponds, streams, sloughs, swamps, and springs. Sexually mature males range in size from 14.0 to 18.0 mm and occasionally reach 22.0 mm. Sexually mature females reach 14.0 mm and rarely 18.0 mm. Ovigerous females occur from March to September but their occurrence probably varies somewhat with latitude, water temperature, etc. Other pertinent comments on ecology can be found in Bousfield (1958). *Gammarus robustus*, described from Colorado by S.I. Smith (1874), is a synonym of *G. lacustris* as verified by a recent examination of the types of this species by Mills and Bousfield (Mills, 1964).

6. *Gammarus minus* Say, 1818

Type Locality (neotype): Small stream at Gable's Woods, Lancaster, Lancaster Co., Pennsylvania.

This common, widely distributed species is found in cave streams, springs, and spring-runs throughout a large part of the Appalachians, Interior Low plateaus, and Ozarks (Fig. 9). It is especially common in areas composed of limestone and dolomitic bedrock. The range was analyzed in detail in recent papers by Holsinger (1969a), Holsinger and Culver (1970), and Cole (1970b). Although the presently known range of this species is disjunct (see range map) and morphological variation is common (often as great locally as regionally), attempts to find diagnostic differences between regionally defined populations that are great enough or consistent enough to warrant specific recognition have not been successful. Cole's recent approach to this problem (Cole, 1970b) in which four major geographic types were defined, appears to be the most logical solution to date. Cole divided regional populations of *G. minus* into: (1) Eastern, including the Piedmont, Appalachians and Interior Low plateaus; (2) Ozarkian, including the Ozark Plateau of Arkansas and Missouri; (3) post-Kansan, including western Illinois and northeastern Missouri (generally to the east and north of the Ozark Plateau); and (4) Pine Hills region of southern Illinois, designating these populations as a subspecies he called *G. m. pinicollis*. In another paper dealing with the morphological variation in *G. minus*, Holsinger and Culver (1970) demonstrated that the variety *tenuipes* (described by Shoemaker, 1940) was an ecophenotype that did not merit taxonomic recognition. The variety *tenuipes*, referred to as Form 1 by Holsinger and Culver, is a degenerate-eyed, subterranean form that inhabits certain large cave systems of two karst areas in the Applachian valley of Virginia and West Virginia. Detailed information on the morphology and ecology of *G. minus* can be found in recent papers by Minckley and Cole (1963), Holsinger and Culver (1970), Cole (1970b), and Culver (1970). Sexually mature males range in size from 8.0 to 14.0 mm, but usually from 8.0 to 12.0 mm. Sexually mature females range in size from 5.0 to 12.0 mm, but usually from 6.0 to 10.0 mm. Females normally produce from five to 15 eggs per clutch, depending on size; very small females sometimes produce fewer than five eggs and very large females sometimes produce more than 15 but rarely more than 20 eggs.

Two species, *Gammarus propinquus* and *G. purpurascens*, were described by Hay (1902, 1903) from a spring near Mammoth Cave, Kentucky and the resurgence of Nickajack Cave, Tennessee, respectively. Both species were subsequently synonymized with *G. minus* by Shoemaker (1940). A third species, *Gammarus elki*, was described from Benton Co., Arkansas and McDonald Co., Missouri by Reimer (1969), but in the opinion of the writer, this species should also be considered a synonym of *G. minus*. A recent examination of the type series of *G. elki* failed to reveal any significant differences from other Ozarkian populations of *G. minus*. While the type material is somewhat aberrant, it easily falls within the acceptable limits of morphological variation usually attributed to *G. minus*.

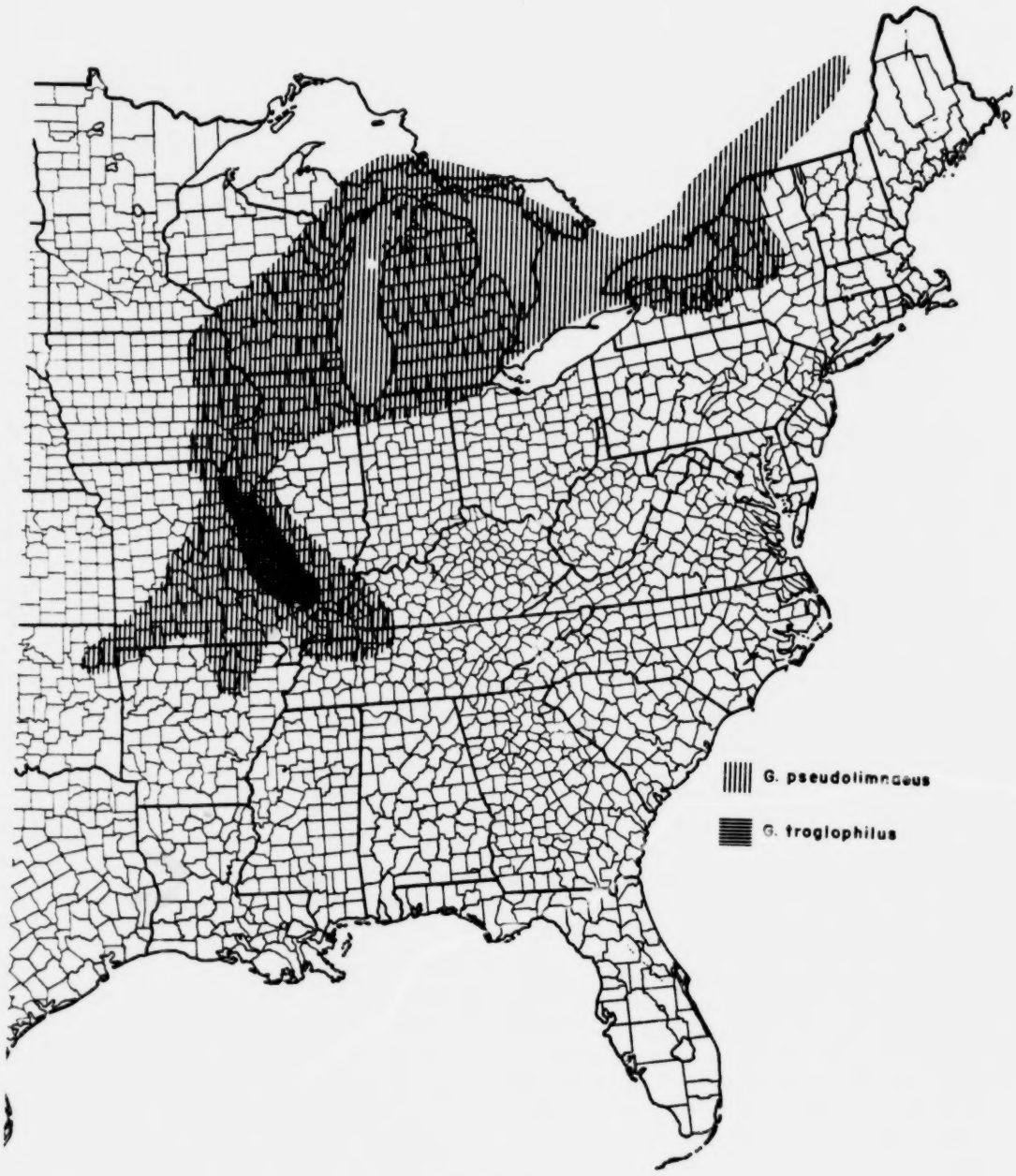


Figure 10. -- Distribution of species of *Gammarus* in North America.

7. *Gammarus pecos* Cole and Bousfield, 1900
Type Locality: Willbank Spring near Fort Stockton, Pecos Co., Texas.
This species was recently described from two localities (a spring and a stream) in the Pecos River drainage of western Texas (Fig. 8). Other than a few brief notes given by Cole and Bousfield in the original description, very little is known about the ecology of this species. Mature males, 12.0 to 14.9 mm; mature females 9.0 to 11.0 mm. *G. pecos* appears to be only one of several closely related species which comprise a species complex that extends from Pecos County north to Chaves, New Mexico. The complex is presently being investigated by G.A. Cole of Arizona State University.

8. *Gammarus pseudolimnaeus* Bousfield, 1958
Type Locality: Rideau River below Hog's Back, Ottawa, Ontario, Canada.
The range of this widely distributed species extends from western Quebec across Ontario into central New York, throughout the Great Lakes region of Michigan, Wisconsin, and Illinois, and west and southwest into eastern Iowa, central Missouri, northeastern Oklahoma, northern Arkansas, western Kentucky, and northwestern Tennessee (Fig. 10). Disjunct records from Prince Georges Co., Maryland (U.S. National Museum collection) and the Texas Coast (Bousfield, 1958) may represent introductions or mislabelled samples, since these sites are far out of the boundaries of the known range. *G. pseudolimnaeus* is rather common in springs and sometimes in cave streams in eastern Iowa, southwestern Illinois, eastcentral Missouri, and northern Arkansas. In the more northern part of its range, especially in the Great Lakes region, it is often found in streams. In springs, this species occurs syntopically with *G. minus* (s. lat.) in Arkansas, eastern Missouri, southwestern Illinois, western Kentucky, and northwestern Tennessee. It is also associated with *G. troglophilus* in southwestern Illinois and eastern Missouri. Sexually mature males reach 17.0 mm; sexually mature females reach 14.0 mm but some may reach maturity at only 6.0 mm.

Ovigerous females have been collected during every season of the year, implying that breeding is continuous throughout the year. According to Bousfield (1958), the life span is approximately 16 months.

9. *Gammarus troglophilus* Hubricht and Mackin, 1940
Type Locality: Morrisons Cave, 2 miles south of Burksville, Monroe Co., Illinois.
This large species is common in cave streams and springs in southwestern Illinois (recorded from 10 counties) and eastern Missouri (recorded from 10 counties) (Fig. 10). It sometimes occurs syntopically with *G. pseudolimnaeus* and *G. minus* (s. lat.), although rarely with the latter in the Missouri part of the range. In Monroe and St. Clair counties, Illinois, this species is sometimes associated with *G. acherondytes*. Largest males reach 24.0 mm; largest females reach 19.0 mm. *G. troglophilus* apparently breeds the year around, as ovigerous females have been collected during every season. Weise (1953), however, in a study of the life cycle and ecology of this species, assumed, on the basis of juvenile frequency, that the breeding season extended from November to April.

## Genus *Crangonyx* Bate, 1859

This genus occurs predominately in North America where it is represented by 18 described species. Approximately 20 to 25 species and subspecies are undescribed. Although eight species have been assigned to *Crangonyx* from outside of North America, only three or four of these appear to be valid members of the genus; the remainder should be assigned to different genera. One of these species, *Cragononyx robertsi* from subterranean habitats in South Africa, constitutes a new genus and is currently being described by Holsinger and Straskraba (in preparation). The species of *Crangonyx* from outside of North America are mostly subterranean forms from Europe (one or two species), the Urals of the USSR (one species), and the Ussuri River basin of the USSR (one species).

The 18 North American species of *Crangonyx* can be assigned to six species groups on the basis of morphological similarities. Bousfield (1958) alluded to some of these groups but did not recognize them formally. Pending a major revision of the genus now in preparation, these groups should be regarded as temporary and not formal taxonomic categories. They are presented here as an aid in delineating possible phyletic lineages within the genus.

1. *Anomalous* group: *C. anomalus*
2. *Forbesi* group: *C. forbesi*
3. *Gracilis* group: *C. floridanus*, *C. gracilis*, *C. packardi* (emended from *packardii*), *C. pseudogracilis*, and *C. rivularis*.
4. *Hobbsi* group: *C. hobbsi*
5. *Obliquus-richmondensis* group: *C. alpinus*, *C. dearolfi*, *C. grandimanus*, *C. obliquus*, *C. richmondensis* s. lat., *C. serratus*, and possibly *C. antennatus*.
6. *Shoemakeri* group: *C. setodactylus*, *C. shoemakeri*, and *C. minor*.

### Key to the North American Species of *Crangonyx*

1 Gnathopodal propods of female proportionately small, palmar margins lined with very small, weak (usually distally un-notched) spines (Fig. 11a); superior lateral setae of gnathopodal propod 2 singly inserted..... 2

Gnathopodal propods of female usually proportionately larger, palmar margins lined with typically strong, distally notched, spine teeth (Fig. 12a,g); superior lateral setae in transverse groups of 1, 2, 3 or more..... 7

2(1) Posterior margins of bases of pereopods 5, 6, and 7 weakly serrate (Fig. 11b); distoposterior margins of abdominal side plates not produced, corners weakly acuminate and nearly truncate in plate 3: *C. rivularis*

Posterior margins of bases of pereopods 5, 6, and 7 distinctly serrate; distoposterior margins of abdominal side plates 2 and 3 produced, corners usually acutely produced..... 3

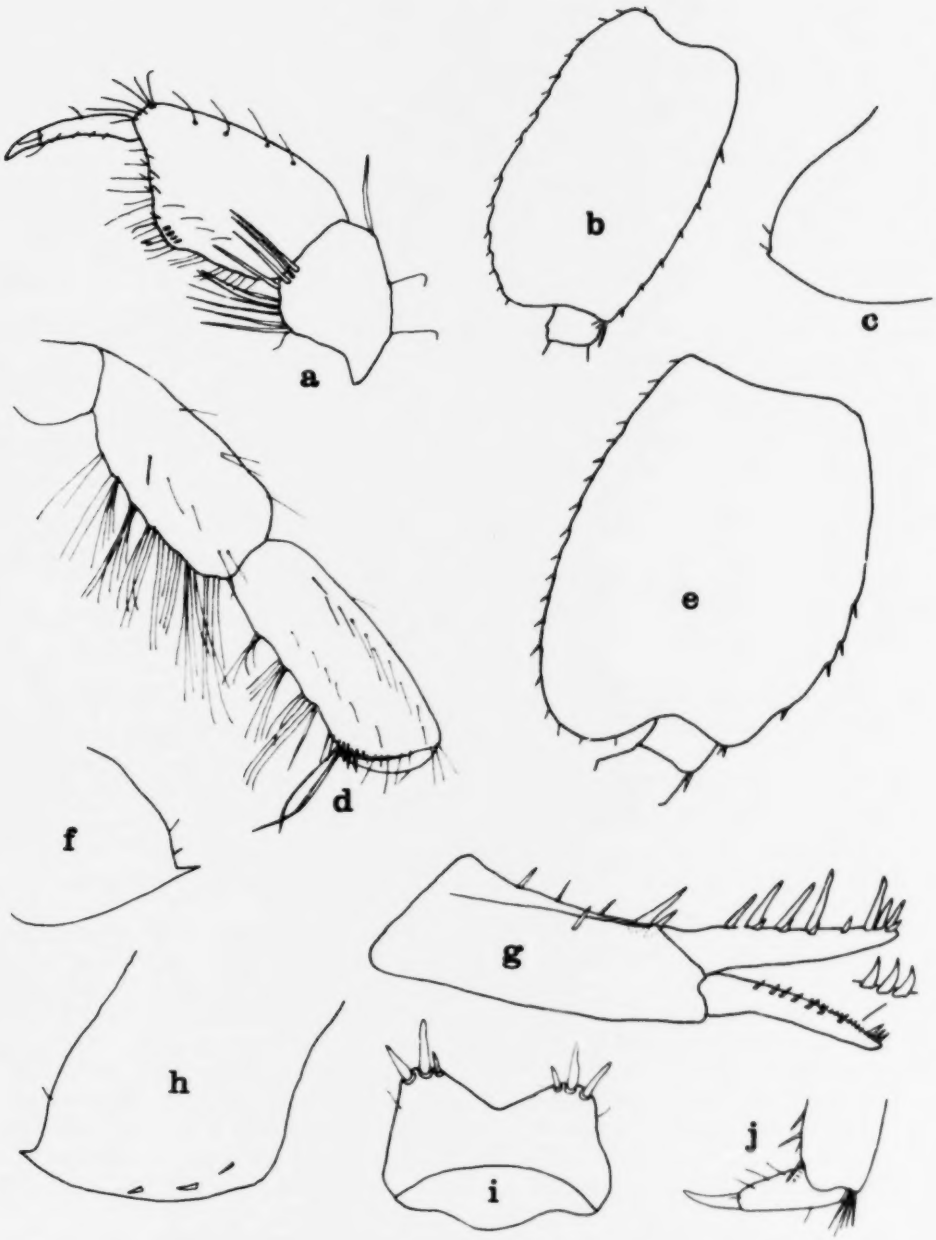


Figure 11. -- Structure of *Crangonyx:* a, 1st gnathopodal propod of female of *C. packardi;* b, basis of pereopod 7 of *C. packardi;* c, abdominal side plate 1 of *C. packardi;* d, gnathopod 2 (in part) of female of *C. hobbsi;* e, basis of pereopod 7 of *C. hobbsi;* f, abdominal side plate 1 of *C. floridanus* (based on Bousfield, 1963b); g, male uropod 2 of *C. shoemakeri;* h, abdominal side plate 2 of *C. pseudogracilis;* i, telson of *C. forbesi;* j, dactyl of pereopod 7 of *C. setodactylus.*

3(2) Gnathopodal propods of female long and narrow, twice as long as broad (Fig. 11d); segment 5 of second gnathopod elongate, longer than segment 6 (propod) in female and as long as propod in male; distoposterior lobe of basis of pereopod 7 large and broadly rounded (Fig. 11e); eyes and pigment degenerate to absent (of subterranean facies): *C. hobbsi*

Gnathopodal propods of female not especially elongate or narrow, segment 5 not as long as propod; distoposterior lobe of basis of pereopod 7 not exceptionally large or broadly rounded; of subterranean facies or not..... 4

4(3) Distoposterior corner of abdominal side plate 1 strongly mucronate (Fig. 11f); sexually mature females reaching 6.5 or 7.0 mm: *S. floridanus*

Distoposterior corner of abdominal side plate 1 weakly mucronate (Fig. 11c); sexually mature females reaching 11.0 mm in epigean forms and 5.0 to 8.0 mm in hypogean forms.....5

5(4) Mature males without row of comb spines on outer ramus of uropod 2 (Fig. 5b): *C. gracilis* complex
(includes a number of closely related undescribed species)

Mature males with row of comb spines on outer ramus of uropod 2 (Fig. 11g)..... 6

6(5) Eyes degenerate or absent; pigment reduced or lacking; distoposterior corner of abdominal side plate 2 very weak: *C. packardi*

Eyes not degenerate, pigment present; distoposterior corner of abdominal side plate 2 strongly acute (Fig. 11h): *C. pseudogracilis* complex
(includes a number of closely related undescribed species)

7(1) Gnathopodal propods of female moderately small, not much expanded distally, palmar margin straight to slightly concave; inner margin of dactyl of female gnathopodal propod 2 with a row of blade-like spines (Fig. 12a); distoposterior corners of abdominal side plates weakly acuminate..... 8

Gnathopodal propods of female moderately large, somewhat expanded distally, palmar margins usually straight or convex; dactyl of female gnathopodal propod 2 without a row of blade-like spines on inner margin (Fig. 12g); distoposterior corners of abdominal side plates acute or not..... 10

8(7) Palmar margin of gnathopodal propod 2 straight; dactyls of pereopods 3-7 with 2 to 3 short, stiff setae on inner margins (Fig. 11j): *C. setodactylus*

Palmar margin of gnathopodal propod 2 concave; dactyls of pereopods 3-7 with typically 1 stiff seta on inner margins... 9

9(8) Mature females with 12 to 15 small, distinct spines on anterior margin of pereopod 7 basis (Fig. 12b); outer ramus of uropod 2 of sexually mature males without inner row of comb spines: *C. minor*

Mature females with only about 8 weak spines on anterior margin of pereopod 7 basis (Fig. 12c); outer ramus of uropod 2 of sexually mature males with inner row of comb spines (Fig. 11g): *C. shoemakeri*

10(7) Propod of gnathopod 2 proportionately very large, nearly 2 times size of 1; bases of pereopods 5, 6, and 7 greatly expanded posteriorly, posterior margin broadly convex and with numerous minute serrations (Fig. 12f); apical lobes of telson with 5 to 6 spines each (Fig. 12k); sexually mature males larger than sexually mature females: *C. anomalus*

Propod of gnathopod 2 larger than 1 but not twice as large; bases of pereopods 5, 6, and 7 not greatly expanded; posterior margins with fewer serrations; apical lobes of telson with 2 to 4 spines each; sexually mature males smaller than sexually mature females:..... 11

11(10) Lacking pigment; eyes degenerate to absent; of subterranean facies..... 15

Eyes and pigment well developed; not of subterranean facies.... 12

12(11) Bases of pereopods 5-7 with deeply serrated posterior margins (Fig. 12e); ventral margin of abdominal side plate 2 of female with up to 11 spines; telson significantly longer than broad, deeply cleft, with spines dorsally as well as apically (Fig. 12j): *C. serratus*

Bases of pereopods 5-7 with shallow serrations in posterior margins; ventral margin of abdominal side plate 2 of female with up to 6 spines; telson not much longer than broad, without dorsal spines..... 13

13(12) Posterior margin of second gnathopodal propod rather long, with 7 to 10 sets of setae; superior lateral setae of second propod in sets of 4 or more (Fig. 12g); posterior margin of basis of pereopod 7 with 16 to 25 fine serrations; distoposterior corners of abdominal side plates small, acute and recessed; uropod 3 rather short, with 3 sets of lateral spines per side; telson short, shallow cleft, with 3 to 4 apical spines per lobe (Fig. 11i): *C. forbesi*

Posterior margin of second gnathopodal propod not so long, with 4 to 6 sets of setae; superior lateral setae of second propod usually in sets of 2's and 3's; posterior margin of basis of pereopod 7 with 10 to 20 moderately deep serrations; distoposterior corners of abdominal side plates produced and acuminate; uropod 3 proportionately longer, with 4 to 5 sets of lateral spines per side; telson about as long as broad, with 2 to 3 apical spines per lobe..... 14

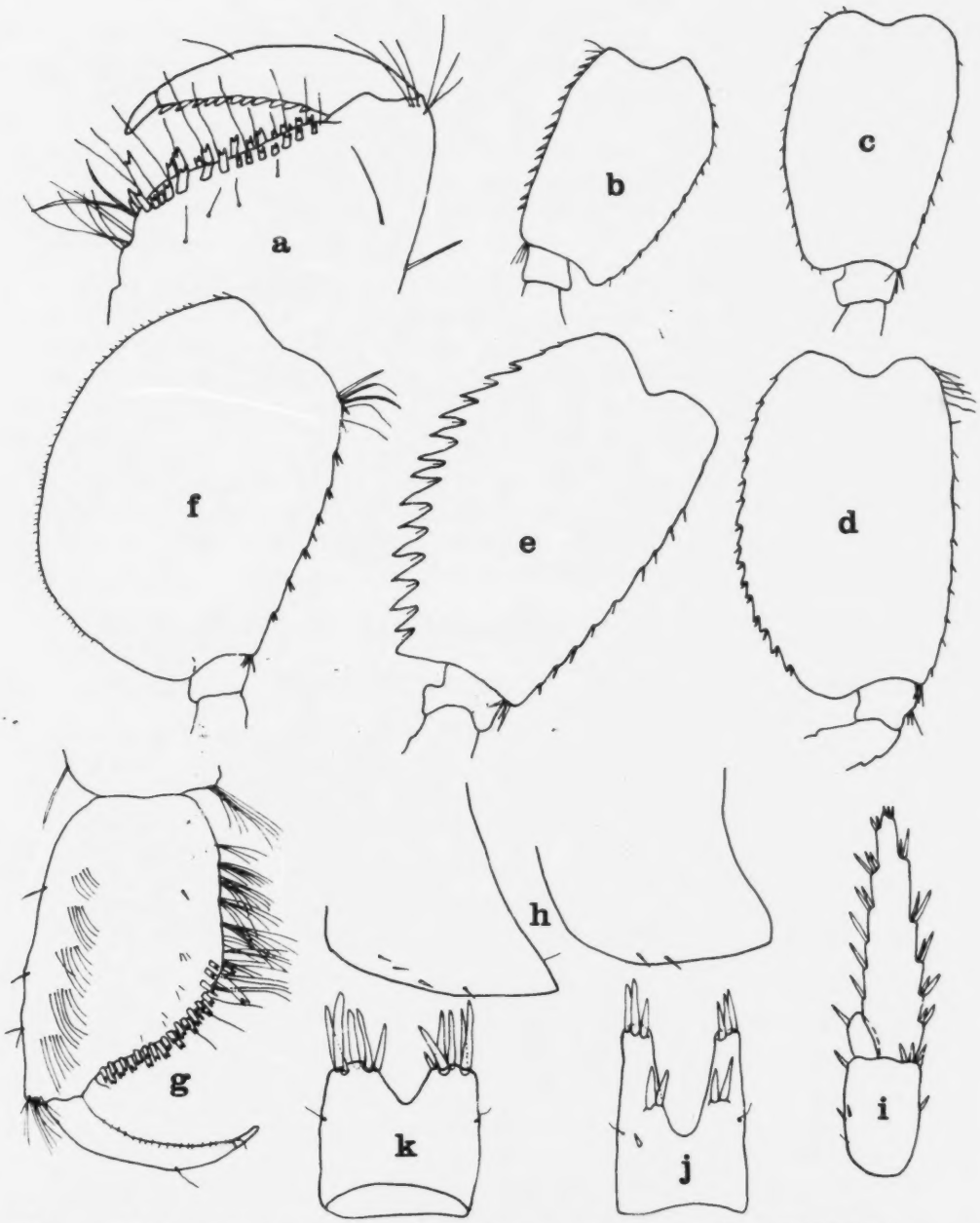


Figure 12. -- Structure of *Crangonyx:* a, female 2nd gnathopodal propod (palmar region) of *C. shoemakeri;* b, basis of pereopod 7 of *C. minor* (based on Bousfield, 1958); c, basis of pereopod 7 of *C. shoemakeri;* d, basis of pereopod 7 of *C. obliquus;* e, basis of pereopod 7 of *C. serratus;* f, basis of pereopod 7 of *C. anomalus;* g, 2nd gnathopodal propod of *C. forbesi;* h, abdominal side plates 2 and 3 of *C. grandimanus;* i, uropod 3 of *C. obliquus;* j, telson of *C. serratus;* k, telson of *C. anomalus.*

14(13) Posterior margin of basis of pereopod 7 with 7 to 9 rather deep serrations; uropod 3 with 4 sets of lateral spines per side; telson shallowly cleft, with 2 apical spines per lobe (based on females only): *C. alpinus*

Posterior margin of basis of pereopod 7 with 10 or more rather deep serrations (Fig. 12d); uropod 3 with 4 to 5 sets of lateral spines per side (Fig. 12i); telson usually more deeply cleft, with 2 to 3 (usually 3) apical spines per lobe: *C. obliquus-richmondensis* complex (including *C. obliquus, C.r. richmondensis, C.r. laurentianus, C.r. occidentalis;* see remarks below)

15(11) Palmar margins of gnathopodal propods oblique and convex; superior lateral setae of propods in sets of 2's and 3's; sexually mature animals from 15.0 to 22.0 mm long.....16

Palmar margins of gnathopodal propods not as oblique, straight to slightly concave; superior lateral setae of propods mostly singly inserted; sexually mature animals 7.0 to 14.0 mm long: *C. antennatus*

16(15) Propod of gnathopod 2 subovate, nearly 2 times size of 1; distoposterior lobe of basis of pereopod 7 large and broadly rounded; abdominal side plates 2 and 3 distinctly produced distoposteriorly (Fig. 12h): *C. grandimanus*

Propod of gnathopod 2 not subovate (broadest distally), not 2 times size of 1; distoposterior lobe of basis of pereopod 7 not broadly expanded; abdominal side plates 2 and 3 not produced distoposteriorly but with small acute corners: *C. dearolfi*

## Annotated List of the Species

1. *Crangonyx alpinus* Bousfield, 1963a
Type Locality: Ledge Lake, Lane Co., Oregon.
This species is known only from alpine lakes in Lane and Douglas counties, Oregon and is described on the basis of mature females (Fig. 18). Largest females = 10.5 mm. Details on the life cycle are not available.

2. *Cragnonyx anomalus* Hubricht, 1943
Type Locality: Spring on Bryan Station Road, 0.3 mile northeast of Eastin Road, 3 miles northeast of Lexington, Fayette Co., Kentucky.
A large, unique species, easily distinguished from all other members of the genus in North America by sexually mature males being larger than sexually mature females. This species is an inhabitant of springs and spring-fed streams in northcentral Kentucky, southeastern Indiana, and southwestern Ohio (Fig. 15). It occurs regularly with *C. setodactylus* (but is much less common) and is sometimes found in company with *C. gracilis* group species and *Synurella dentata*. Largest males = 22.0 mm; sexually mature females, 13.0 to 19.0 mm. Newly hatched young = 2.0 mm. Ovigerous females are found in winter and early spring but little other information is available on the life cycle.

3. *Crangonyx antennatus* Packard, 1881
Type Locality: Nickajack Cave, Marion Co., Tennessee.
This rather common troglobitic species ranges from the upper Tennessee River basin in Lee, Scott, and Wise counties, Virginia south-southwestward to northeastern Georgia (into the upper Alabama River basin) and west along the Tennessee River valley to northwestern Alabama and extreme southcentral Tennessee; it is also in the Sequatchie River valley of Tennessee (Holsinger, 1969a) (Fig. 13). The eyes of this species are degenerate (a few pigmented specks) to absent. *C. antennatus* occurs in cave pools and small cave streams and is especially common in the caves of Lee Co., Virginia and Claiborne Co., Tennessee, where it is often associated with the troglobitic isopod *Asellus recurvatus*. Sexually mature males range in size from 4.5 to 10.0 mm but most are between 5.0 and 8.0 mm. Sexually mature females range in size from 5.5 to 13.5 mm but the average is between 7.0 and 10.0 mm. Newly hatched young = 1.5 mm. Life span is of at least three years and perhaps longer. In the northern part of the range at least, continuous breeding throughout the year is indicated by the presence of ovigerous females during all four seasons. Apparently only a very small percentage of the individuals of a given population can breed at any one time (Holsinger, in preparation).

4. *Crangonyx dearolfi* Shoemaker, 1942a
Type Locality: Hobo Cave, Warnersville, Berks Co., Pennsylvania.
This rare troglobitic species is occasionally found in caves of southeastern Pennsylvania (four caves) and central Maryland (three caves) (Fig. 13). It occurs in cave pools (some of which are temporary) and has degenerate eyes. Sexually mature males, 15.0 mm; sexually mature females, 19.0 to 22.0 mm. Newly hatched young = 3.5 mm. Virtually nothing is known about the life cycle except that a single ovigerous female was collected in January from a cave in Maryland.

5. *Crangonyx floridanus* Bousfield, 1963b
Type Locality: Cypress swamp, Highlands Hammock State Park, Highlands Co., Florida.
This species is disjunctly distributed from central Florida (Highlands County) through western Florida (Jackson County) to eastern Louisiana (St. Tammany Parish) (Fig. 15). A possible subspecies occurs in groundwater habitats in southern Florida (i.e., a well near Miami). *C. floridanus* inhabits swamps, ponds, and cave pools. Specimens from caves often have smaller (degenerate) eyes. This species is rather common in Gerards Cave, Jackson Co., Florida, where it is found in pools, and, on one occasion, was removed from the gut of the troglobitic salamander *Haideotriton wallacei*. Sexually mature males, 3.0 to 8.0 mm; sexually mature females, 5.0 to 10.0 mm. Ovigerous females have been collected during the months of February through October, thus indicating that breeding possibly occurs the year around.

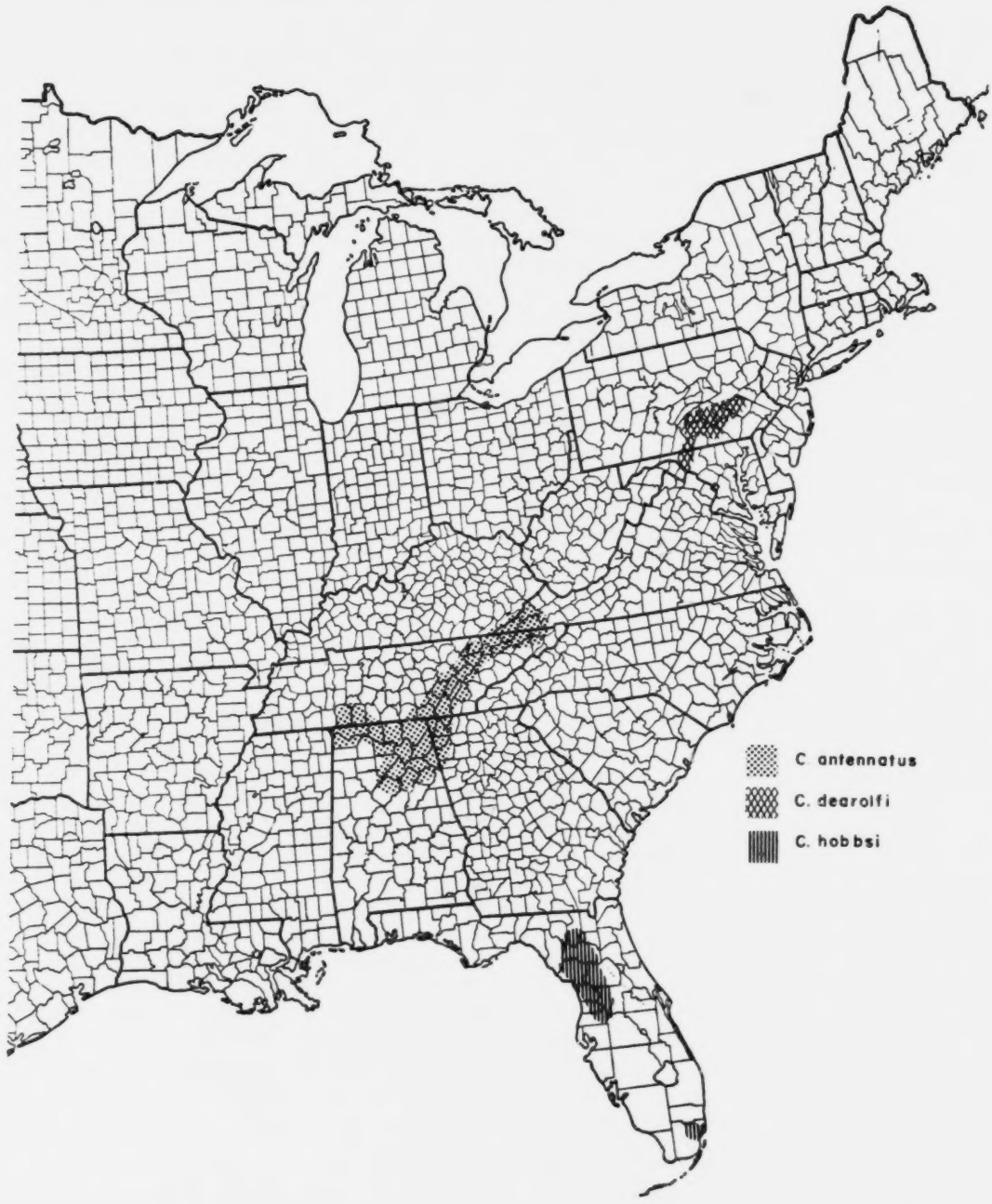


Figure 13. -- Distribution of species of *Crangonyx* in North America.

6. *Crangonyx forbesi* (Hubricht and Mackin, 1940)
Type Locality: Outlet of drain, Osage Hills Golf Course, Kirkwood, St. Louis Co., Missouri.
A rather large, somewhat variable species that is common in cave streams, springs, and occasionally in small surface streams and ponds in eastcentral Missouri and southwestern Illinois (Fig. 14). Populations from similar habitats in southcentral and southwestern Missouri, northern Arkansas, and northeastern Oklahoma, all referred to this species by Hubricht and Mackin (1940) and Hubricht (1943), differ from *C. forbesi* s. str. in several important characters and may represent a closely related, undescribed species. *C. forbesi* is commonly associated with *Gammarus troglophilus* and occasionally with *Gammarus acherondytes* and *Bactrurus brachycaudus* in the cave streams of southern Illinois and eastern Missouri. This species is about as common in springs as it is in caves and does not show an appreciable loss of pigment or eye structure when it occurs in caves. The size is quite variable; sexually mature males range from 10.0 to 18.0 mm and sexually mature females from 14.0 to 22.0 mm. Newly hatched young = 2.0 to 3.0 mm in length. Ovigerous females are known from all four seasons, implying that breeding is continuous throughout the year. A possible subspecies of *C. forbesi* occurs to the east of Illinois and is found in westcentral Kentucky, southwestern Ohio, and central and southern Indiana. This form inhabits caves and springs and differs from *C. forbesi* s. str. only in a few minor points.

7. *Crangonyx gracilis* S.I. Smith, 1871
Type Locality: Lake Superior near St. Ignace Island, Ontario, Canada.
Bousfield (1958) summarized most of the useful information on this species and clarified its vague status. The range limits of *C. gracilis* are still not known precisely, and, for this reason, a range map is not included. Bousfield (1958) published a number of valid records from Ontario and Quebec, Canada and pointed out that this species probably ranges throughout the Great Lakes drainage basin, occurring in lakes, permanent ponds, pools, streams and swamps. The writer has seen additional samples from Ohio and Wisconsin. Numerous collections from the eastern and southeastern United States have been identified as *C. gracilis* and many of these have been published as records for the species (Hubricht and Mackin, 1940; Hubricht, 1943). However, it is the writer's opinion (as well as that of Bousfield) that *C. gracilis* s. lat. represents a complex of species and subspecies and that *C. gracilis* s. str. (in the sense of S.I. Smith, 1871 and Bousfield, 1958) is probably restricted to the Great Lakes region. Many of the published references to this species (in addition to those of Hubricht) are in error. At least one closely related species occurs in the Truckee River of western Nevada, while another undescribed form occurs in swamps and pools in the Tidewater area (Coastal plain) of southeastern Virginia. In *C. gracilis* s. str., sexually mature males range in size from 4.5 to 6.5 mm and sexually mature females from 6.0 to 10.5 mm. Nothing specific is known about the life cycle of this species.

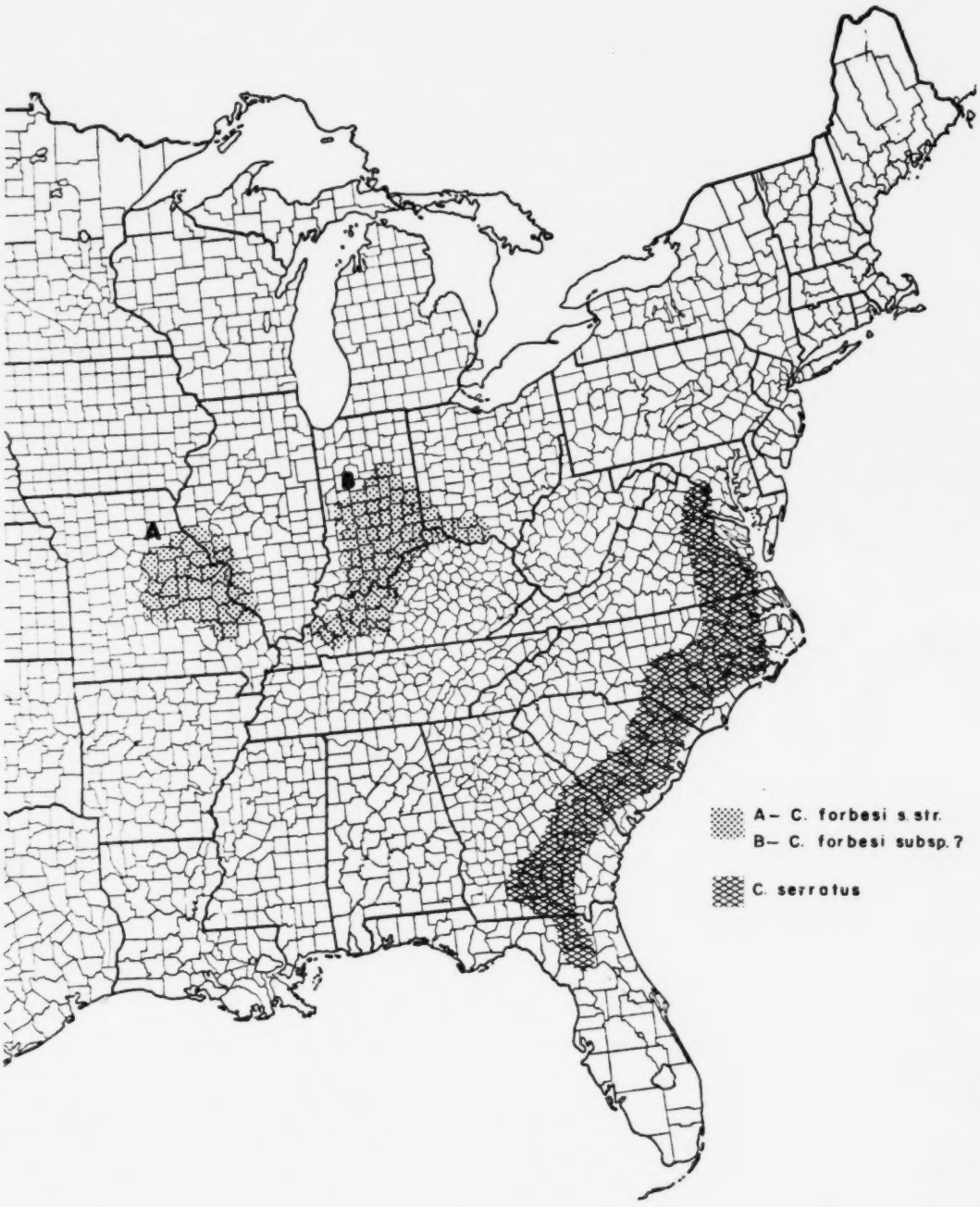


Figure 14. -- Distribution of species of *Crangonyx* in North America

Figure 15. -- Distribution of species of *Crangonyx* in North America

Figure 16. -- Distribution of species of *Crangonyx* in North America.

Figure 17. -- Distribution of species of *Crangonyx* in North America

8. *Crangonyx grandimanus* Bousfield, 1963b
Type Locality: Indian Cave, 7 miles southwest of Ocala, Marion Co., Florida.
This large, distinct troglobitic species is known only from three localities, two caves and one well in central and southern Florida (Fig. 16). In the structure of its gnathopods and mouth parts, this species appears to be closely related to *Crangonyx obliquus*. *C. grandimanus* is often associated with *C. hobbsi*, but the latter is usually more abundant. Sexually mature males, 8.0 to 13.0 mm; sexually mature females, 10.0 to 15.0 mm. Ovigerous females have been collected during February, March and December and sexually mature females have also been noted in October samples. Apparently breeding is continuous throughout the year but additional biological data are very sketchy at the moment.

9. *Crangonyx hobbsi* Shoemaker, 1941
Type Locality: Huggins Cave, Alachua Co., Florida.
This very distinct, rather highly specialized troglobitic species is easily distinguished by the narrow, elongate fifth and sixth segments of the gnathopod propods (especially in the female). *C. hobbsi* is known from caves and wells in the central limestone region of Florida and from a well in Dade Co., Florida (Fig. 13). It is sometimes associated with *C. grandimanus*, the latter being much less common. Largest males, 9.0 mm; sexually mature females, 7.0 to 11.0 mm. Breeding apparently takes place the year around but ovigerous females are never abundant at any given time.

10. *Crangonyx minor* Bousfield, 1958
Type Locality: Stony Creek, 4 miles west of Tillsonburg, Oxford Co., Ontario, Canada.
This species is closely related to *C. shoemakeri* but can be distinguished from the latter by the lack of comb spines on the outer ramus of uropod 2 of the male and by its geographic distribution. *C. minor* inhabits a variety of aquatic habitats, including small streams (temporary and permament), sloughs, ditches, drains, springs, and ponds. It appears to be more common in small streams than in other habitats, however. This species is recorded from southeastern Iowa, central Illinois, westcentral Indiana, with disjunct populations in southern Illinois, southeastern Michigan, northwestern Missouri, and southern Ontario (Fig. 19). Many of Hubricht's 1943 middlewestern United States records for *C. shoemakeri* were actually this species. Sexually mature males, 5.0 to 8.5 mm; sexually mature females, 8.5 to 12.5 mm. Ovigerous females occur from March to June but little else is known about the biology of this species.

Figure 18. -- Distribution of species of *Crangonyx* in North America.

11. and 12. *Crangonyx obliquus-richmondensis* complex, including:
a) *Crangonyx obliquus* (Hubricht and Mackin, 1940)
Type Locality: Small creek west of the college chapel, Clarksville, Johnson Co., Arkansas.
b) *Crangonyx richmondensis richmondensis* Ellis, 1940
Type Locality: Pond on Richmond Plantation, Cordesville, Berkeley, Co., South Carolina.
c) *Crangonyx r. occidentalis* Hubricht and Harrison, 1941
Type Locality: Echo Lake, just south of King Co. line, Washington.
d) *Crangonyx r. laurentianus* Bousfield, 1958
Type Locality: Black Lake, Gatineau Park near Kingsmere, Quebec, Canada.
The present systematic status of *C. obliquus* vis-a-vis *C. richmondensis* is unclear. Hubricht and Mackin (1940) described *C. obliquus* from a single female taken from a small creek in Johnson Co., Arkansas. Ellis (1940) described *C. richmondensis* from specimens taken from a pond in Berkeley Co., South Carolina. Hubricht (1943) synonymized *C. richmondensis* with *C. obliquus* and listed numerous new records for *C. obliquus* from the eastcentral and southeastern United States (Fig. 17). Bousfield (1958) did not agree with Hubricht, however, and resurrected *C. richmondensis* from synonymy, giving reasons (based on descriptions of these species and not on examination of type material) for its status as a separate taxon. Bousfield (1958) also recognized three subspecies of *C. richmondensis* -- *C. r. richmondensis* from the eastern United States and Canada; *C. r. laurentianus* from Michigan, southcentral Ontario and western Quebec (Fig. 17) and *C. r. occidentalis* (formerly considered a full and separate species) from British Columbia and Washington state (Fig. 18).

During the preparation of this manual, the writer examined numerous collections of *obliquus-richmondensis* group material and reached the following conclusions. The material from the vicinity of the type locality of *C. obliquus* is very similar to the topotypic material of *C. richmondensis*. Despite a slight variation in the shape of the gnathopodal propods of both sexes, there is no significant taxonomic difference between the Arkansas populations and the South Carolina ones. The slight variation noted in the structure of the gnathopods may be clinal and worthy of subspecific recognition, but this is still unclear amd must await further study. The material from Nova Scotia and Newfoundland assigned to *C. r. richmondensis* by Bousfield (1958) and material subsequently examined by the writer from New England differs in several minor but consistent ways from topotypic material of *C. richmondensis* from South Carolina and may well constitute a distinct subspecies. The populations of the Great Lakes region, designated *C. r. laurentianus* by Bousfield (1958), are also subspecifically distinct as described. Moreover, several populations from central New York appear to be intergrades between the Great Lakes *laurentianus* form and the New England-southeastern Canada *richmondensis* form. Several other, possibly isolated, population clusters of *C. richmondensis* s. lat. occur in the eastcentral and eastern United States (see range map), but their specific or subspecific status is still vague. The populations from

southwestern Canada and northwestern United States (i.e., *C. r. occidentalis*) may well represent a separate species from the eastern form(s) of *C. obliquus-richmondensis*. Other than minor morphological differences, already pointed out by Bousfield (1958), these populations are geographically far removed and presumably well isolated from the eastern races. It is apparent, in view of the results of the writer's recent investigation, that the taxonomy of the *obliquus-richmondensis* group will have to be revised before anything more definitive can be said about it.

The following notes on ecology and biology apply to the eastern and eastcentral races of the *C. obliquus-richmondensis* complex (i.e., excluding *C. r. occidentalis*, details about which can be found in Bousfield (1958). Sexually mature males, 7.5 to 11.0 mm; sexually mature females, 12.0 to 20.0 mm. Newly hatched young = 2.0 to 3.0 mm. This form occurs in a variety of habitats, including small streams (temporary and permanent), sloughs, swamps and bogs, ditches, ponds, drains, and in the shallow margins of small (often acidic) lakes. Ovigerous females occur from about January to June, after which only immature amimals are found throughout the summer and fall. Life span of about one year. See also papers by Sprules (1967) and Judd (1963) for pertinent information on the ecology of this species in Canada. In the southern United States, *C. obliquus* (s. str.?) is often found in company with an undescribed species of the *Crangonyx gracilis* group and *Synurella bifurca*. The populations of *C. richmondensis* from South Carolina are often associated with *Crangonyx serratus*.

13. *Crangonyx packardi* S.I. Smith, 1888
Type Locality: Wells at Orleans, Orange or Lawrence Co., Indiana.
Although this species was regarded by Hubricht (1943) as a subspecies of *C. gracilis*, it is clearly a distinct subterranean species, and one, which, after careful study, may turn out to be a complex of closely related species and/or subspecies. Material from the vicinity of the "type locality" in southern Indiana was studied and proved useful in determining the validity of this species. The range of this species extends throughout most of the cave and karst regions of southern Indiana and central Kentucky (Fig. 16). *C. packardi* is found in pools and small streams of caves where it is often associated with isopods (*Asellus* spp.) and *Stygobromus* spp. (in Kentucky). A form, possibly subspecifically distinct from *C. packardi*, occurs in the caves of the Bluegrass area of northcentral Kentucky. Other subspecies, or perhaps very closely related species, occur in caves and other subterranean habitats in northeastern Kentucky and southern Ohio, in southern Illinois, and in eastern Kansas. A distinct, but related species, inhabits caves along the western margin of the Cumberland Plateau in Kentucky. Based on the presence of comb spines on the outer ramus of the second uropod of the male, *C. packardi* s. str. appears to be more closely related to *C. pseudogracilis* than to *C. gracilis*. The following ecological notes are based on southern Indiana-central Kentucky cave populations (*C. packardi* s. str.). Sexually mature males, 4.5 to 7.5 mm; sexually mature females, 4.0 to 8.5 mm (possibly reaching sexual maturity at a smaller size in the more northern parts of the range). Newly

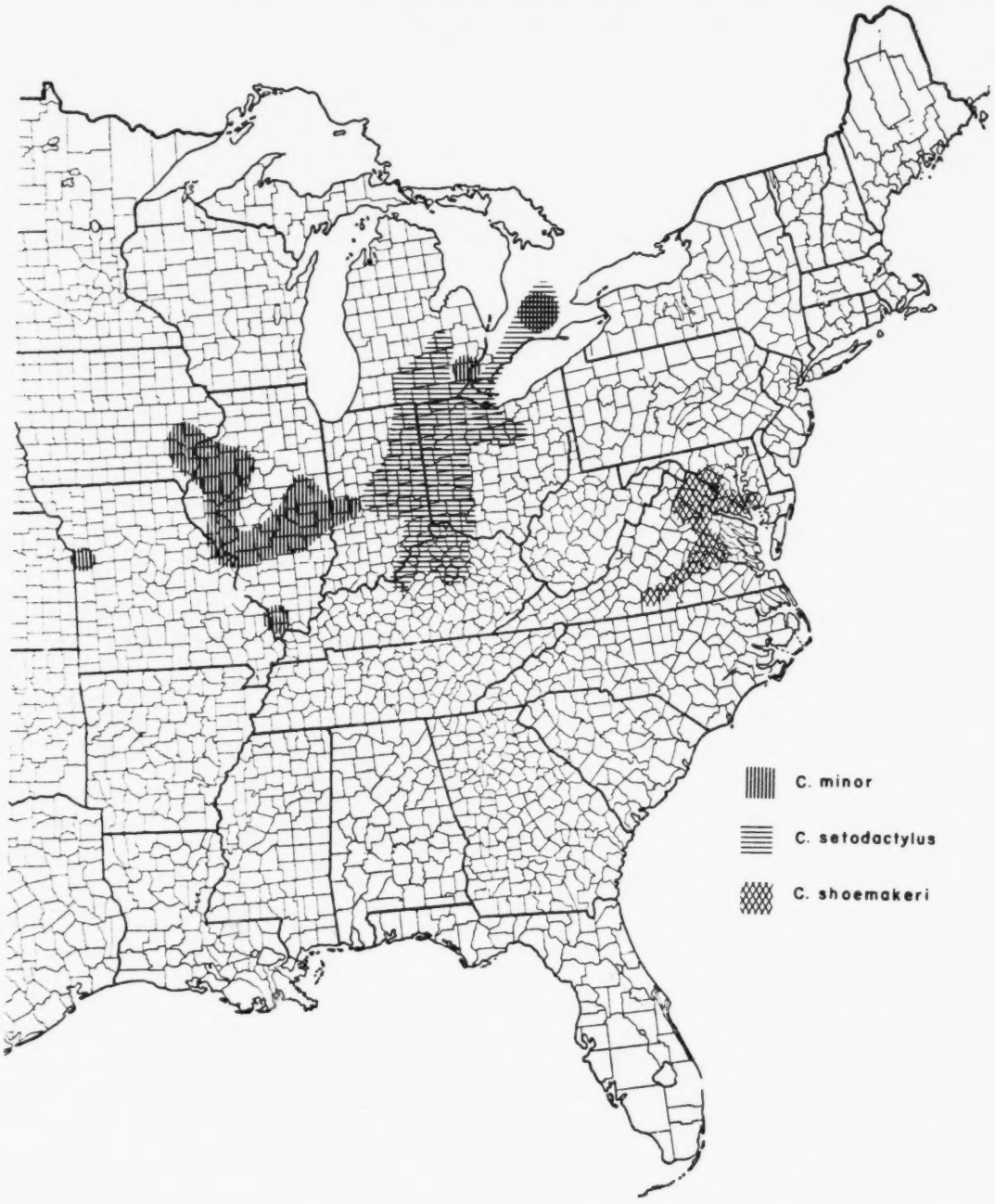


Figure 19. -- Distribution of species of *Crangonyx* in North America

hatched young = 1.5 mm. Ovigerous females have been observed during all seasons of the year, indicating that breeding is continuous throughout the year as is apparantly true of most of the other subterranean species of the genus.

14. *Crangonyx pseudogracilis* Bousfield, 1958
Type Locality: Napanee River at Napanee, Lennox and Addington Co., Ontario, Canada.
As pointed out by Bousfield (1958), this species was previously confused with the superficially similar *C. gracilis*. The presence of a row of comb spines on the outer ramus of the second uropod of the male, combined with several more subtle characters (see Bousfield, 1958), serve to differentiate this species from *C. gracilis*, however. The presently known range of *C. pseudogracilis* is spotty but indicates a wide distribution in the United States and southern Canada. Outside of the range given by Bousfield (1958), this species has been reported from Oregon by Bousfield (1961) and from Connecticut by Mills (1964) (Fig 20). The writer has also seen several collections from as far south as Mississippi which have many characters in common with *C. pseudogracilis* s. str. Further, more critical examination may well reveal that *C. pseudogracilis* is a complex of several very closely related species. Therefore, at the moment it is impossible to accurately delimit the range of this species with any more certainty than is shown on the distribution map herein. Data on the ecology of this species have been usefully summarized by Bousfield (1958) and will not be repeated here. Sexually mature males, 4.5 to 6.5 mm (and possibly to 9.0 rarely); sexually mature females, 7.5 to 10.5 mm.

15. *Crangonyx rivularis* Bousfield, 1958
Type Locality: Rocky Saugeen River, 4 miles north of Durham, Grey Co., Ontario, Canada.
This species is to date known only from southeastern Ontario, Canada (Fig. 15) and nothing new has been added on its ecology and distribution since first reported by Bousfield (1958). Sexually mature males, 3.5 to 4.5 mm; sexually mature females, 5.5 to 7.0 mm.

16. *Crangonyx setodactylus* Bousfield, 1958
Type Locality: Spitler Creek, 4 miles north of Norwich, Oxford Co., Ontario, Canada.
This rather large species of the *shoemakeri* group is easily distinguished from all other species of the genus by the presence of two to three short, stiff setae on the inner margin of the dactyls of pereopods 3-7 Many of the records listed by Hubricht (1943) for *C. shoemakeri* from the eastcentral United States (especially Kentucky, Indiana and Ohio) are actually this species. The range of *C. setodactylus* extends from southeastern Ontario south and west across southern Michigan through western Ohio, eastern Indiana and into northcentral Kentucky (Fig. 19). In Ontario, Michigan and possibly in Indiana, its range overlaps with that of *C. minor* to which it is closely related. This species is found in a variety of cold-water habitats, including small streams, outlets of drains, springs, sloughs and temporary pools. *C. setodactylus* is very

common in the springs and spring runs of northern Kentucky (Bluegrass region) and southwestern Ohio, where it is usually associated with *Synurella dentata*, and sometimes with *Crangonyx anomalus* and *Crangonyx* spp. of the *gracilis* group. In these associations, *C. setodactylus* is usually first in the order of abundance, followed by *S. dentata*. *C. anomalus* and *C.* spp. are usually much less abundant. Sexually mature males, 8.0 to 12.0 mm; sexually mature females, 10.0 to 17.0 mm. Breeding in most populations appears to occur in the winter, followed by ovigerous females in the spring (March to May or June). The newly hatched young are released in the late spring and immatures occur during the summer and fall. Occasionally, however, breeding may take place in the fall as indicated by a collection from a spring in Kentucky that was made in November and contained ovigerous females. Life cycle of probably one year.

18. *Crangonyx shoemakeri* (Hubricht and Mackin, 1940)
Type Locality: Pools along the Potomac River, 2 miles west of Georgetown, Washington, D. C.
This species is closely related to *C. minor* and *C. setodactylus* but is easily distinguished from these species by the presence of a row of comb spines on the outer ramus of the second uropod of the male and by other differences noted in the accompanying key. The range of this species extends from southcentral Maryland south and southwest along the Piedmont and western margin of the Coastal Plain to southcentral Virginia (Fig. 19). *C. shoemakeri* is an inhabitant of temporary pools and ponds (often with grassy bottoms), springs, small streams, and bogs. Sexually mature males, 5.5 to 9.5 mm; sexually mature females, 9.0 to 13.5 mm. Ovigerous females occur from February to May, followed by immatures during the summer. Life cycle of about one year.

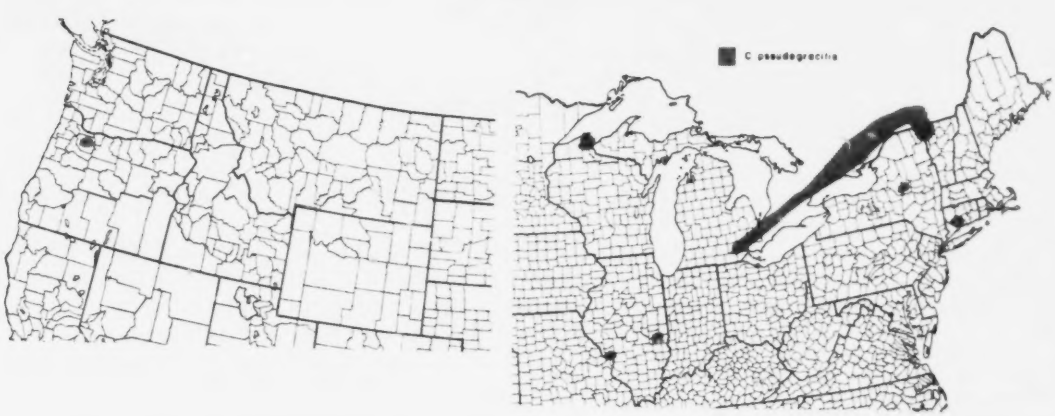


Figure 20. -- Distribution of species of *Crangonyx* in North America.

## Genus *Synurella* Wrzesniowski, 1877

This genus is widespread in the Holarctic region but is represented by a greater number of species in Europe and Asia than in North America. Only four of approximately 18 described species occur in North America and only three of these are found in the contiguous United States; the other species (*Synurella johanseni* Shoemaker, 1920) is known from Alaska. Although several of the European species are represented in subterranean waters, none of the North American forms are known to be subterranean or troglobitic.

*Synurella* bears a superficial resemblance to *Crangonyx* but can be distinguished easily by the short, uni-ramous third uropod and the rather narrow, deeply cleft telson. Juveniles of the three species of the United States undergo a peculiar developmental phenomenon in which the gnathopodal propods bear a large, distal spine or process. This process decreases with increase in size and disappears at maturity.

### Key to the North American Species of *Synurella* (excluding Alaska)

1 Palmar margins of gnathopodal propods distinctly concave (Fig. 21a); uronites fused; mature males larger than mature females; sexually mature specimens from 7.5 to 19.0 mm: *S. dentata*

Palmar margins of gnathopodal propods straight to only slightly concave (Fig. 21b); uronites fused or not; mature males smaller than mature females; sexually mature specimens from 5.0 to 14.0 mm ..... 2

2(1) Uronites fused; sexually mature specimens from 6.0 to 14.0 mm: *S. bifurca*

Uronites not fused (free); sexually mature specimens from 5.0 to 12.0 mm: *S. chamberlaini*

### Annotated List of the Species

1. *Synurella bifurca* (Hay, 1882)

Type Locality: Rivulet following into the Noxubee River at Macon, Noxubee Co., Mississippi.

This species is principally an inhabitant of the Mississippian embayment region and is distributed from southeastern Missouri and western Tennessee through eastern and southern Arkansas into Louisiana, west into southeastern Texas and east through Mississippi into western Alabama (Fig. 22). *S. bifurca* is found in small streams, temporary ponds and pools, springs, seeps, ditches, and sloughs. Ovigerous females occur from December to May or June; immatures only in late summer and fall. Life cycle of one year. Sexually mature males, 6.0 to 10.5 mm; sexually mature females, 7.5 to 14.0 mm. Newly hatched young are 1.5 mm. Larger females produce from 140 to 215 eggs per brood.

2. *Synurella chamberlaini* (Ellis, 1941)
Type Locality: Pond on the Richmond Plantation, 2.4 miles south of Cordesville, Berkeley Co., South Carolina.
This species is distributed from Maryland southward along the Atlantic Coastal Plain to South Carolina (Fig. 22). It is an inhabitant of small streams, bogs, ponds, and ditches and is often associated with *Crangonyx* spp. Ovigerous females occur in winter and spring; immatures only during the late summer and fall. Life cycle of one year. Sexually mature males, 5.0 to 8.5 mm; sexually mature females, 6.0 to 12.0 mm (the majority being 7.0 to 10.0 mm). Sexual maturity is reached at a slightly smaller size in the southern part (Carolinas) of the range. Ovigerous females brood up to 65 eggs per clutch and newly hatched young are 1.5 mm.

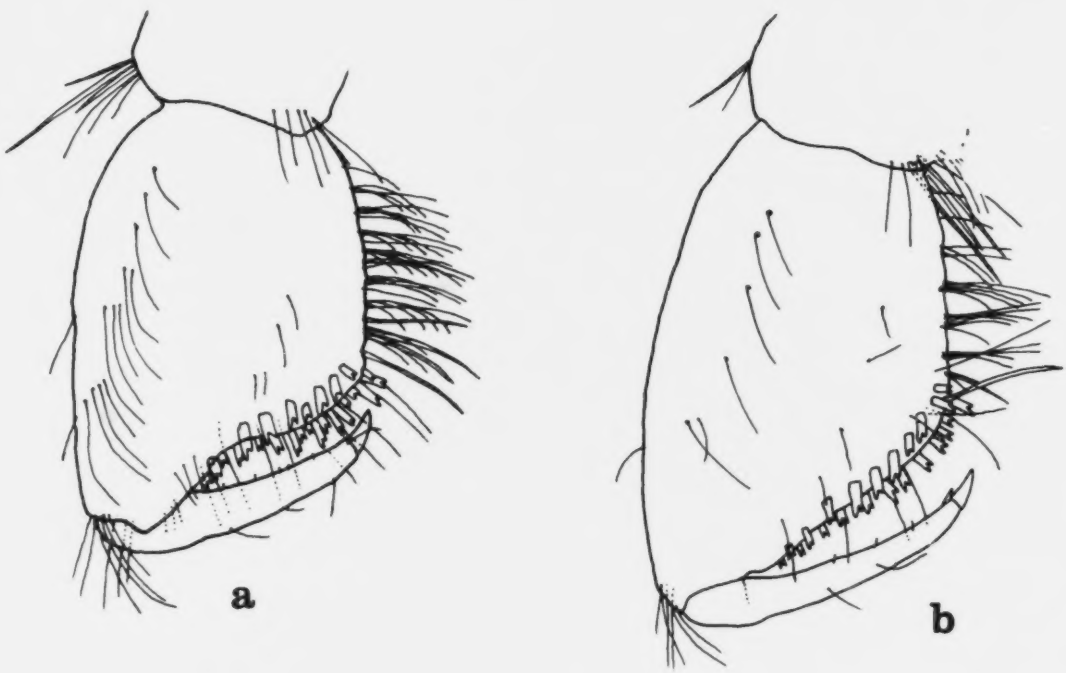


Figure 21. -- Structure of *Synurella:* a, 2nd gnathopodal propod of male of *S. dentata*; b, 2nd gnathopodal propod of male of *S. bifurca*.

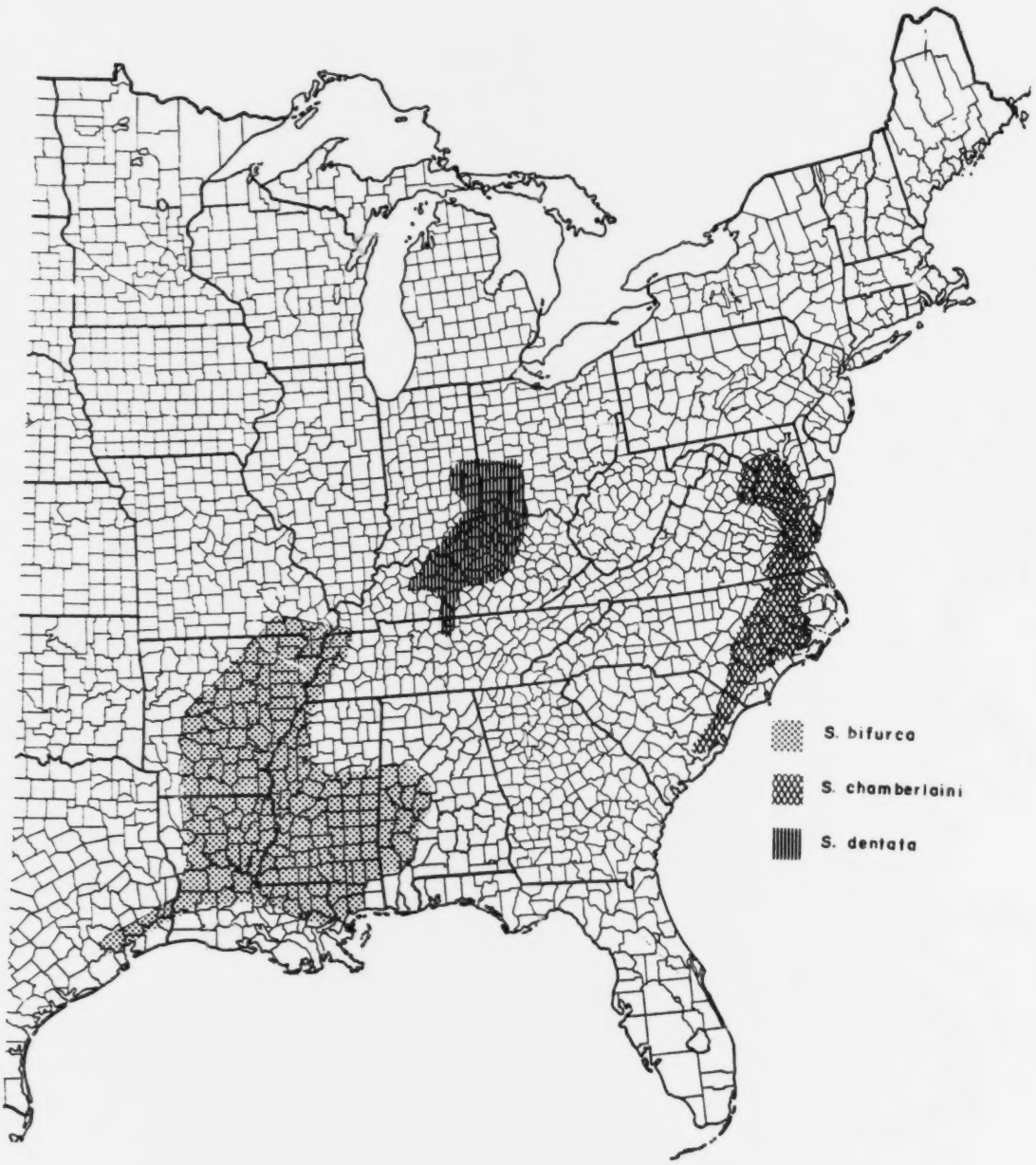


Figure 22. -- Distribution of species of *Synurella* in North America (excluding Alaska).

3. *Synurella dentata* Hubricht, 1943
Type Locality: Small spring in a barnyard near an old mansion, 2.9 miles south-southwest of Jimtown, Fayette Co., Kentucky.
This species is easily distinguished from the above by the males being larger than the females at sexual maturity and the concave palmar margins of the gnathopodal propods. *S. dentata* inhabits springs and small streams (mostly spring-fed) and ranges from southeastern Indiana to southern Ohio, south into Kentucky and as far south as northcentral Tennessee (Fig. 22). This species is very common in springs and spring runs of the Bluegrass region of northcentral Kentucky where it is commonly associated with *Crangonyx setodactylus* and less frequently with *Crangonyx anomalus* and *Crangonyx* sp. (*gracilis* group). Sexually mature males, 10.0 to 19.0 mm (most between 11.0 and 13.0 mm); sexually mature females, 7.5 to 15.0 mm (average is 9.0 to 11.0 mm); newly hatched young = 1.5 mm. Ovigerous females produce up to 125 eggs per brood and occur in late fall, winter and early spring. Immatures are found throughout the year with seasonal peaks.

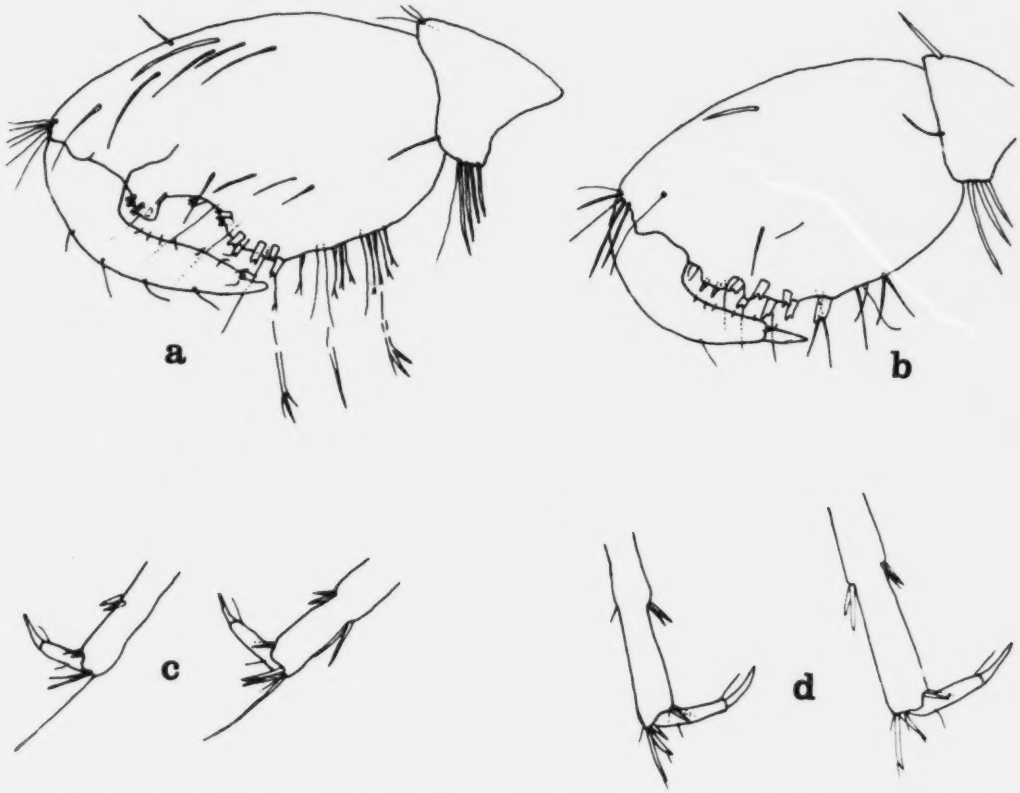


Figure 23. -- Structure of *Apocrangonyx* (based on Holsinger, 1969b); a, 2nd gnathopodal propod of male of *A. araeus;* b, 2nd gnathopodal propod of male of *A. subtilis;* c, dactyls and distal ends of propods of pereopods 6 and 7 of *A. parvus;* d, dactyls and distal ends of propods of pereopods of *A. ephemerus*.

## Genus *Apocrangonyx* Stebbing, 1899

The genus *Apocrangonyx* is composed of six described and seven undescribed small, cryptic subterranean species, most of which have very narrowly defined ranges. Five of the six described species are keyed out below. The undescribed species are known from caves in the Appalachian region (three from West Virginia, two from Alabama, one from Tennessee and one from Georgia) and are apparently quite rare and highly insular in distribution. Two of the described species (i.e., *A. ephemerus* and *A. parvus*), along with the three undescribed species from West Virginia, have several important characters in common with Appalachian species of *Stygonectes* and may be reassigned to this genus in a future revision by the writer. Since two recent papers by Holsinger (1969a, 1969b) treated the distribution of the species of this genus in detail, range maps will not be repeated.

### Key to the Species of *Apocrangonyx*

*A. lucifugus* is not included for reasons given below and elsewhere (Holsinger, 1969b).

1 Propod of gnathopod 2 larger than 1 (especially in mature males); posterior margin of gnathopodal propod 1 with marginal setae ..... 2

Propod of gnathopod 2 about equal in size to propod 1 in both sexes; posterior margin of gnathopodal propod 1 without setae ..... 4

2(1) Palmar margin of gnathopodal propod 2 of male with deep excavation (Fig. 23a); distoposterior corners of abdominal side plates of female well developed, subacute; telson and uropod 1 of male slender and elongate: *A. craeus*

Palmar margin of gnathopodal propod 2 of male without deep excavation; distoposterior corners of abdominal side plates of female poorly developed, rounded; telson and uropod 1 of male normal, not elongate..... 3

3(2) Palmar margin of gnathopodal propod 2 of male with 2 median processes (Fig. 23b); lateral sternal processes bifurcate; lateral spines absent on inner ramus of uropod 1: *A. subtilis*

Palmar margin of gnathopodal propod 2 of male without median processes; lateral sternal processes simple (not bifurcate); lateral spines present on inner ramus of uropod 1: *A. nortoni*

4(1) Distal ends of pereopodal propods 5-7 with 1 very long seta each (Fig. 23c); apical margin of telson with 9 to 10 spines; sexually mature females up to 2.7 mm long: *A. parvus*

Distal ends of pereopodal propods 5-7 without elongate setae (Fig. 23d); apical margin of telson with 6-8 spines; sexually mature females up to 5.0 mm long: *A. ephemerus*

## Annotated List of the Species

1. *Apocrangonyx araeus* Holsinger, 1969b
Type Locality: Seep, 1.0 miles south of Crittenden, Nansemond Co., Virginia.
A very unique, interstitial species that inhabits groundwater seeps and small springs in the Tidewater area of southeastern Virginia and extends from Matthews County south to Norfolk Co. (now Norfolk City) and southwestward to Nansemond county. Sexually mature males reach 7.0 mm; sexually mature females, 3.5 to 5.5 mm. Newly hatched young = 1.0 mm. Ovigerous females in late winter and early spring and perhaps throughout the year but samples from summer and fall are not available.

2. *Apocrangonyx ephemerus* Holsinger, 1969b
Type Locality: Tawneys Cave, Giles Co., Virginia.
This species is known from mud-bottom, drip pools in two caves in the Sinking Creek valley of Giles Co., Virginia. Sexually mature males, 3.4 mm; sexually mature females, 3.5 to 5.0 mm.

3. *Apocrangonyx lucifugus* (Hay, 1882)
Type Locality: Well in Abingdon, Knox Co., Illinois.
Since type material does not exist and attempts to collect "topotypes" have been unsuccessful, the status of this species remains vague. *A. lucifugus* may be conspecific with *A. subtilis* (see Holsinger, 1969b for further comments).

4. *Apocrangonyx nortoni* Holsinger, 1969b
Type Locality: Ingram Cave, Clay Co., Tennessee.
This species is known only from the type locality, where it was collected from a seepage pool. Largest males, 3.85 mm; largest females (sexually mature), 3.5 mm. Other biological data are not available.

5. *Apocrangonyx parvus* Holsinger, 1969b
Type Locality: Crawford Cave No. 2, Randolph Co., West Virginia.
This tiny species is known authenticially only from the type locality where it was found in two mud-bottom drip and seep pools. A second record (Cassell-Windy Cave, Pocahontas Co., West Virginia) given by Holsinger (1969b) was based on a single specimen, but on further examination appears to represent another species. Largest males, 2.5 mm; largest females (sexually mature), 2.7 mm. This is the smallest described species of Gammaridae from North America. Two of the undescribed species of *Apocrangonyx* from West Virginia reach sexual maturity at an even smaller size, however.

6. *Apocrangonyx subtilis* Hubricht, 1943
Type Locality: Small seep, 5.0 miles southwest of Pomona, Jackson Co., Illinois.
This is the widest ranging species of the genus and extends from Adams Co., Illinois south-southeastward to Union Co., Illinois and west to St. Genevieve Co., Missouri. This species is known from both seeps and cave pools. Ovigerous females are available from April collections and sexually mature specimens have been observed in collections from

October and November. Breeding may continue the year around but only a few females are ovigerous at a given time. Sexually mature males, 4.0 to 5.0 mm; sexually mature females, 3.0 to 4.5 mm.

## Genus *Stygonectes* W. P. Hay, 1903

Synonym = *Synpleonia* Creaser, 1934.

The genus *Stygonectes* contains 29 described and nine undescribed subterranean species, which occupy groundwater habitats from Vermont and New York south and southwestward to Texas and Oklahoma. The genus was treated in detail in a recent monographic revision by Holsinger (1967), and many additional data on the group can be found there. All but one of the undescribed species have been collected since the generic revision in 1967 and will be described in a future paper by the writer (in preparation). Distributional maps for the species can be found in Holsinger (1967, 1969a) and are not included in the manual. The range maps published by the writer in 1969 were for central Appalachian species and reflect most of the data acquired on the genus subsequent to the 1967 revision.

### Key to the Species Groups of *Stygonectes*

The following key to species groups; keys to individual species within these groups can be found in Holsinger (1967) and will not be repeated here.

1 Propod of gnathopod 1 often stouter but otherwise about equal in size to 2; pereopod 6 and 7 about equal in length; sexually mature males typically smaller than sexually mature females.. 2
Propod of gnathopod 1 stouter and usually larger than 2; pereopod 7 a little longer than 6 (excepting one rare species); sexually mature males larger than sexually mature females ..... 5

2(1) Posterior margin of gnathopodal propod 1 rather short, without setae (excepting one rare species); posterior angle of gnathopodal propod 1 with 2 to 6 large, unequal but typically curved spines on outside (Fig. 24a); posterior margins of abdominal side plates convex (Fig. 24b) ..... 3
Posterior margin of gnathopodal propod 1 with 3 to 5 groups of setae; posterior angle of gnathopodal propod 1 with 1 large and usually straight spine on outside (Fig. 24e); posterior margins of abdominal side plates weakly convex to relatively straight (Fig. 24f) ..... 4

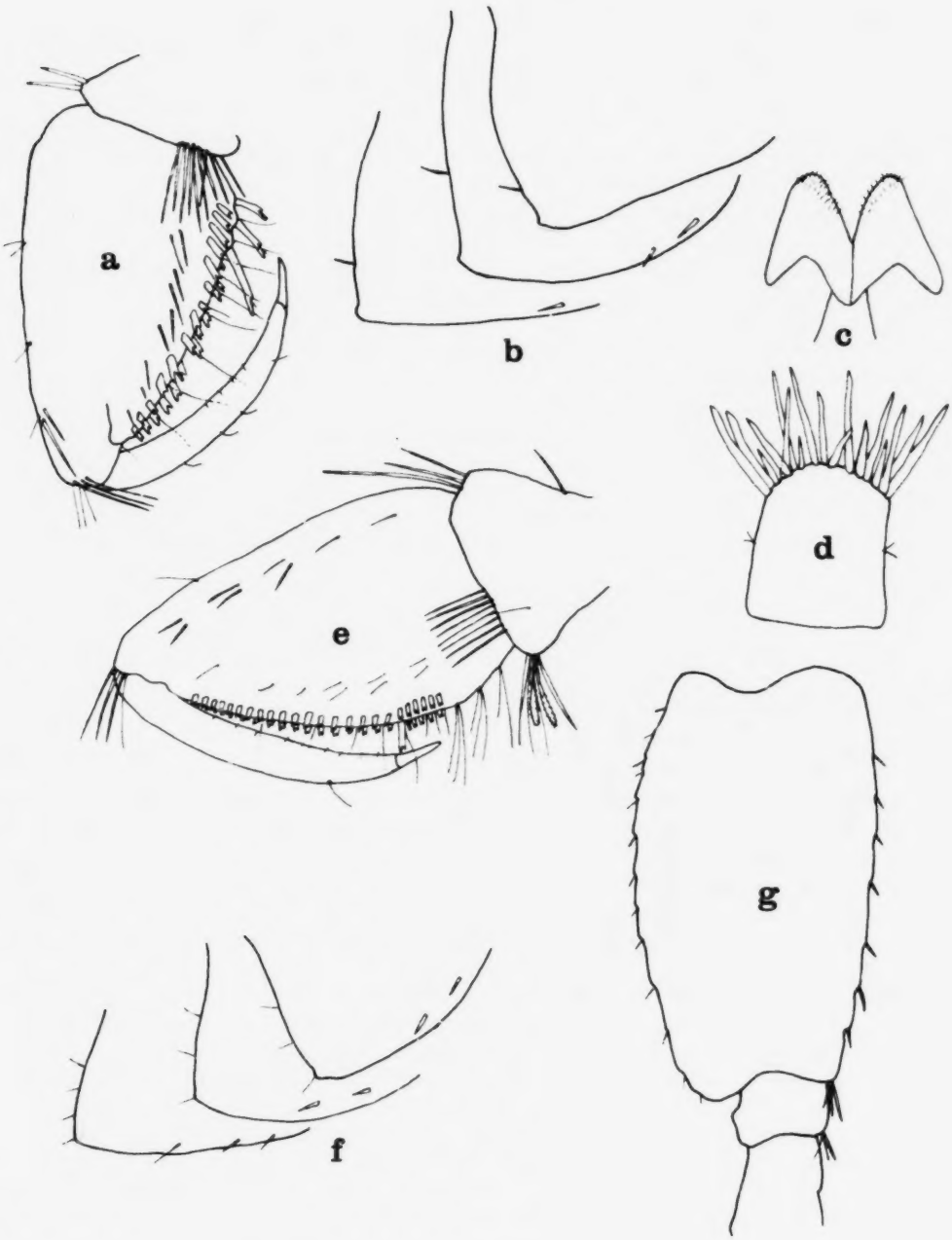


Figure 24. -- Structure of *Stygonectes*: a, 1st gnathopodal propod of *S. emarginatus;* b, abdominal side plates of *S. emarginatus;* c, lower lip of *S. spinatus* (based on Holsinger, 1967); d, telson of *S. spinatus* (based on Holsinger, 1967); e, 1st gnathopodal propod of *S. flagellatus;* f, abdominal side plates of *S. longipes;* g, basis of pereopod 7 of *S. emarginatus*.

3(2) Inner lobes of lower lip vestigial or absent (Fig. 24c); distoposterior lobes of pereopod bases rather well defined; posterior margins of abdominal side plates with up to 10 setae; telson without lateral spines, apical margin convex (Fig. 24d);..... *spinatus* group *(S. spinatus)*

Inner lobes of lower lip not vestigial but sometimes small; distoposterior lobes of pereopod bases usually rather poorly defined or nearly absent (Fig. 24g); posterior margins of abdominal side plates with up to 6 (but often fewer than 6) setae; telson with lateral spines and without excavation in apical margin, or without lateral spines and with or without shallow excavation in apical margin..... *emarginatus* group

4(1) Coxal plate of pereopod 4 enlarged (Fig. 25a); bases of pereopods 5-7 broadly expanded posteriorly, distoposterior lobes broad and well defined; apical margin of telson entire or with shallow excavation; telson without lateral spines.....
.....*hadenoecus* group

Coxal plate of pereopod 4 not enlarged (Fig. 25c); bases of pereopods 5-7 not greatly expanded posteriorly, distoposterior lobes rather small or poorly defined; telson rather long, with or without lateral spines, apical margin without excavation (Fig. 25b)..... *flagellatus* group

5(1) Propod of gnathopod 1 up to twice the size of propod of gnathopod 2, propod palmar margin of sexually mature males with a prominent distal notch or shallow excavation (Fig. 25d); basis of pereopod 7 of larger males with a prominent ventrally produced distoanterior lobe (Fig. 25f); telson with lateral spines.....*pizzinii* group

Propod of gnathopod 1 larger but not twice as large as propod of gnathopod 2; propod palmar margin of sexually mature males without distal notch or excavation; larger males without a prominent distoanterior lobe on pereopod 7 (Fig. 25e); telson with lateral spines in only 2 species.....*tenuis* group

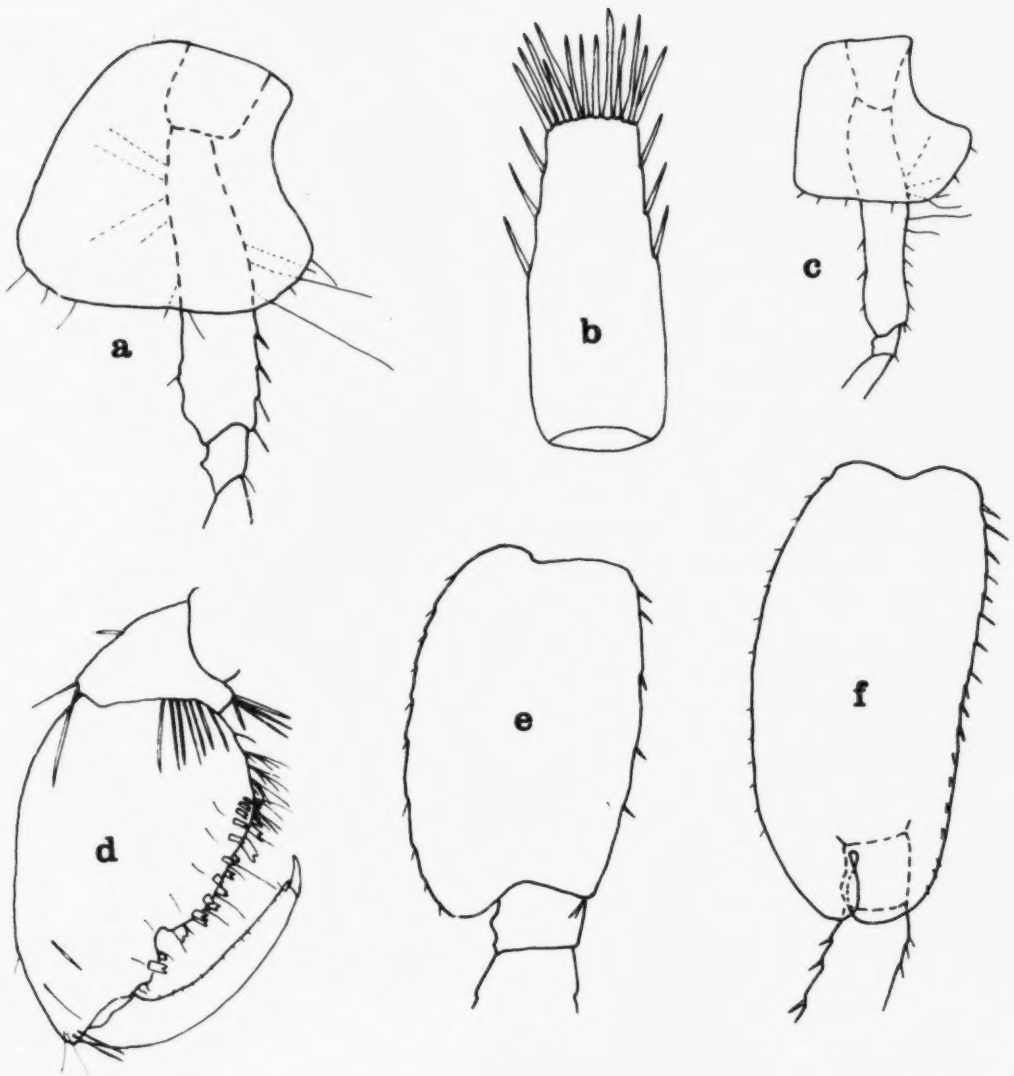


Figure 25. -- Structure of *Stygonectes*: a, coxal plate of *S. hadenoecus*; b, telson of female of *S. flagellatus*; c, coxal plate of *S. flagellatus* (based on Holsinger, 1966); d, 1st gnathopodal propod of male of *S. indentatus*; e, basis of pereopod 7 of *S. alabamensis*; f, basis of pereopod 7 of male of *S. indentatus*.

## Annotated List of the Species

Species are arranged within species groups in the same order as they were presented in Holsinger (1967). Individual species are treated in detail only where new data have been obtained since the 1967 revision.

*Emarginatus* group

1. *Stygonectes emarginatus* (Hubricht, 1943)
Type Locality: Organ Cave section of Greenbrier Caverns, Greenbrier Co., West Virginia.
This species occupies small cave streams and sometimes pools. In the caves of the Greenbrier valley of West Virginia, it is often found in company with *Stygonectes spinatus*, *Gammarus minus* and the isopod *Asellus holsingeri* (see Culver, 1970 for further details on this ecological relationship). The range extends from western Maryland (Garrett County) south-southwestward through the Appalachian valley and along the eastern margin of the Appalachian Plateau to Monroe Co., West Virginia. Sexually mature males, 9.0 to 10.5 mm; sexually mature females, 9.0 to 14.0 mm. Sexually mature females have been observed in spring and summer and ovigerous females have been collected in August. However, adult-sized animals have been found the year around, suggesting that breeding may be continuous.

2. *Stygonectes mundus* Holsinger, 1967
Type Locality: Witheros Cave, Bath Co., Virginia.
This species was described from only three specimens, none of which were completely mature. For reasons given elsewhere (Holsinger, 1969a), which were based on examination of material subsequent to 1967, the writer considers this form to be a probable subspecies of *Stygonectes emarginatus*.

3. *Stygonectes morrisoni* Holsinger, 1967
Type Locality: Witheros Cave, Bath Co., Virginia.
Although this species was originally described from a series of specimens collected from a single cave (Witheros Cave), it has subsequently been found farther to the north in Pendleton Co., West Virginia and possibly in Hardy Co., West Virginia. The latter, however, may represent a closely related species or subspecies (Holsinger, 1969a). In the type locality, *Stygonectes morrisoni* occurs syntopically with *Stygonectes mundus* (s. str.), where it is apparently much more abundant. Largest male, 6.0 mm; sexually mature females, 6.0 to 8.0 mm. Ovigerous females have been collected in the early spring but little else is known about the biology of this species.

4. *Stygonectes cooperi* Holsinger, 1967
Type Locality: Silers Cave, Berkeley Co., West Virginia.
This species is known only from two males, the largest of which is 6.0 mm. Morphologically, *Stygonectes cooperi* shows rather close affinity with several species of *Stygobromus* and may be reassigned to this genus in the future. The species inhabits small, mud-bottom seep pools in the type locality.

5. *Stygonectes stellmacki* Holsinger, 1967
Type Locality: Millers Cave, Centre Co., Pennsylvania.
This rather unique species was originally described from a single male (14.25 mm) but subsequent collecting has resulted in the discovery of two females (the largest being 15.40 mm). *Stygonectes stellmacki* occurs in a shallow, mud-bottom pool in the type locality but nothing else is known about its ecology.

6. *Stygonectes gracilipes* Holsinger, 1967
Type Locality: Skyline Caverns, Warren Co., Virginia.
This rather large, distinct species ranges from southern Franklin Co., Pennsylvania south-southwestward through the Shenandoah Valley to Rockingham Co., Virginia. It is an inhabitant of cave pools and occasionally small cave streams. Sexually mature males, 9.0 to 10.5 mm; sexually mature females, 10.0 to 18.0 mm. Adult specimens are found in various populations the year around but ovigerous females are currently known only from a January sample.

7. *Stygonectes conradi* Holsinger, 1967
Type Locality: Butler-Sinking Creek Cave, Bath Co., Virginia.
This small cavernicolous species, closely related to *Stygonectes gracilipes*, is known only from its type locality. Although the species was originally described from females (largest, 8.25 mm), two small males were recently obtained from the type locality and are morphologically similar to the females. *Stygonectes conradi* is found in gravels in the cave stream where it is extremely rare and is associated with snails (*Fontigens*) and isopods (*Asellus*), the last two groups being much more common.

*Spinatus* group

8. *Stygonectes spinatus* Holsinger, 1967
Type Locality: Court Street Cave, Greenbrier Co., West Virginia.
This species inhabits caves of the Greenbrier valley and extends from central Pocahontas Co. south to central Monroe Co., West Virginia. At least one subspecies occurs in the caves around Greenville, West Virginia (westcentral Monroe County). *Stygonectes spinatus* is found in the gravels of small streams and in small cave pools; it is often associated with *Stygonectes emarginatus*, *Gammarus minus*, and *Asellus holsingeri* (see above and also Culver, 1970). Sexually mature males, 3.5 to 5.5 mm; sexually mature females, 4.3 to 7.5 mm. Adults have been observed during every season of the year and ovigerous females have been taken during the spring, summer, and fall. Breeding apparently takes place year round, with only a small percentage of the mature females producing young at a given time.

*Pizzini* group

9. *Stygonectes pizzinii* (Shoemaker, 1938)
Type Locality: Wetzels Spring, Glover Archbold Parkway, Washington, D. C.
This species is recorded from a series of groundwater habitats (caves, springs, seeps and wells) in the Piedmont and is distributed from Fairfax

Co., Virginia northeastward to Chester and Lancaster counties, Pennsylvania. The range is discontinuous between Howard Co., Maryland and Lancaster Co., Pennsylvania. Sexually mature males, 8.0 to 18.75 mm; sexually mature females, 7.5 to 15.75 mm. In general, animals reach sexual maturity at a larger size and attain a greater length in the Reftons Cave (Lancaster Co., Pennsylvania) population than anywhere else in the range (see Holsinger, 1967 for a possible explanation). Sexually mature adults, ovigerous females and juveniles are found the year around indicating that reproduction is continuous in this species.

10. *Stygonectes indentatus* Holsinger, 1967
Type Locality: Outlet of drain, 3 miles northwest of Suffolk, Nansemond Co., Virginia.
An interstitial species, somewhat smaller than, but closely related to, *Stygonectes pizzinii*. This species is known from two drains in Nansemond Co., Virginia and one seep in adjoining Isle of Wight Co., Virginia. Sexually mature males, 7.5 to 9.75 mm; sexually mature females, 6.0 to 7.5 mm. Nothing is known about the life cycle except that ovigerous females were observed in a January collection.

*Tenuis* group

11. *Stygonectes tenuis* s. lat.--two subspecies are recognized as follows:
a) *S. t. tenuis* (Smith, 1874)
Type Locality: Wells at Middletown, Middlesex Co., Connecticut.
This subspecies is disjunctly distributed in groundwater habitats (wells and seeps) from central Connecticut southwestward to the Maryland peninsula.
b) *S. t. potomacus* Holsinger, 1967
Type Locality: Bog in Burleith Woods, Georgetown, Washington, D. C.
This subspecies differs slightly but consistently from *S. t. tenuis* in lacking coxal gills on pereopod 7 (both sexes) and sternal processes on the pleonite of the male. It is rather common in groundwater habitats (especially in seeps and small wet-weather bogs) in the vicinity of Washington, D. C. The range extends from central Maryland (west of the Chesapeake Bay) westward to the Blue Ridge Mountains and south to the vicinity of Richmond, Virginia). The biology of *S. tenuis* s. lat. can be summarized as follows: Sexually mature males, 9.0 to 16.5 mm (but rarely larger than 12.0 mm); sexually mature females, 5.5 to 9.75 mm. Ovigerous females have been found in winter, spring and summer collections and mature adults and juveniles occur in collections the year around. Reproduction may be continuous.

12. *Stygonectes allegheniensis* Holsinger, 1967
Type Locality: Spring, Ilion, Herkimer Co., New York.
A wide-ranging, somewhat variable species found in a variety of subterranean habitats (i.e., especially caves, wells, and springs) of the Appalachian Plateau of central and southern New York, westcentral Pennsylvania and western Maryland, the Valley and Ridge of central Pennsylvania, and the Piedmont of southeastern Pennsylvania. Sexually mature

males, 8.0 to 13.5 mm; sexually mature females, 5.25 to 13.0 mm. Ovigerous females from March through November and possibly all year around. This species is a common cavernicole in the small pools of the caves of Albany and Schoharie counties, New York.

13. *Stygonectes hayi* (Hubricht and Mackin, 1940)
Type Locality: Small spring, south end of National Zoological Park, Washington, D. C.
This species is known only from its type locality where it occurs synotopically with *S. tenuis potomacus*. Largest males, 9.75; largest females, 10.0 mm.

14. *Stygonectes alabamensis* s. lat.--two subspecies as follows:
a) *S. a. alabamensis* (Stout, 1911)
Type Locality: Well, 1 mile east of P.O., Auburn, Lee Co., Alabama.
This wide ranging subspecies is distributed from southcentral Alabama westward to eastcentral Mississippi and then northwestward to southwestern Tennessee, then westward across northern Arkansas to eastern Oklahoma and north to central Missouri. The species is somewhat variable morphologically as well as ecologically and occupies a variety of groundwater biotopes, including seeps, springs, wells, and caves.
b) *S. a. occidentalis* Holsinger, 1967
Type Locality: seeps, 2.3 miles south of Fittstown, Pontotoc Co., Oklahoma.
This subspecies is sparsely distributed in groundwater outlets (seeps and springs) from Tulsa Co., Oklahoma soutnward through the Arbuckle Mountains to Dallas Co., Texas and possibly eastward to Union Co., Louisiana. The biology of *S. alabamensis* s. lat. can be summarized as follows: Sexually mature males, 9.0 to 13.5 mm; sexually mature females, 6.0 to 13.0 (but usually not exceeding 10.0 mm). Ovigerous females have been taken in the spring and fall but sexually mature specimens are known from all seasons of the year.

15. *Stygonectes montanus* Holsinger, 1967
Type Locality: Springs, Rich Mtn., Rich Mtn. Station, Polk Co., Arkansas.
This species is known only from its type locality and virtually nothing is known about its biology. There is some evidence to indicate that this species may be a peripherally isolated, highly aberrant form of *Stygonectes alabamensis* and not a distinct species as originally indicated by Holsinger (1967). The true status of this species must await further study, however.

16. *Stygonectes elatus* Holsinger, 1967
Type Locality: Seep, 0.2 mile east of The Lodge, Magazine Mtn., Logan Co., Arkansas.
This species is known only from its type locality, where it is apparently uncommon. A number of other seeps on Magazine Mountain contain populations of *Stygonectes alabamensis* but not *Stygonectes elatus*.

17. *Stygonectes barri* Holsinger, 1967
Type Locality: Seep, 0.5 mile east of Greenville, Wayne Co., Missouri.
Outside of the type locality, this species is known only from an intermittent stream in Madison Co., Missouri. Sexually mature males, 10.5 to 12.75 mm; sexually mature females, 6.5 to 8.5 mm. Collections are available only from April, at which time ovigerous females were observed.

18. *Stygonectes balconis* Hubricht, 1943
Type Locality: Boyetts Cave, Hays Co., Texas.
Outside of the type locality, this species is known only from Irelands Cave (Travis County) which is situated 25 miles north-northeast of the former. Largest males, 16.0 mm; largest females, 9.75 mm to 12.50 mm. Ovigerous females are unknown to date; most of the specimens collected have been males.

19. *Stygonectes bifurcatus* Holsinger, 1967
Type Locality: Gorman Cave, San Saba Co., Texas.
This species ranges from Kendall County north-northeastward through Travis County to Coryell County and then westward through Lampasas County to San Saba County. *Stygonectes bifurcatus* usually occurs in cave pools and is sometimes found syntopically with *Stygonectes russelli* (see below). Sexually mature males, 13.0 to 19.0 mm; sexually mature females, 11.0 to 14.0 mm. Newly hatched young = ca. 2.0 mm. Mature specimens have been collected during spring, summer and fall but ovigerous females are presently known only from collections made in the spring and summer.

20. *Stygonectes russelli* Holsinger, 1967
Type Locality: Tippits Cave, Coryell Co., Texas.
This highly variable cavernicolous species is recorded from seven counties in the eastern and eastcentral portion of the Edwards Plateau region of Texas. There are geographic clusters of populations and several significant gaps in the range, and this, coupled with the variable morphology of the species, strongly indicates a polytypic species or perhaps a species complex (Holsinger, 1967). Even though a number of collections have been made since 1967, the problem is still far from being resolved. *S. russelli* inhabits shallow cave pools and small streams and sometimes occurs syntopically with *S. bifurcatus* and rarely with *S. balconis* and *S. dejectus*. Sexually mature males, 7.5 to 10.0 mm; sexually mature females, 5.5 to 14.0 mm. Newly hatched young = ca. 2.0 mm. Sexually mature specimens and juveniles have been collected during all seasons of the year and ovigerous females are known from winter, spring and summer. Like many other cavernicolous amphipod species, *S. russelli* probably breeds the year around.

21. *Stygonectes reddelli* Holsinger, 1966
Type Locality: Whiteface Cave, San Saba Co., Texas.
This species is known only from five females collected from the type locality. Larger females, apparently sexually mature are 12.0 to 13.50 mm.

22. *Stygonectes clantoni* (Creaser, 1934)
Type Locality: Well on Clanton Farm, 4 miles southeast of Ottawa, Franklin Co., Kansas.
This large subterranean species is known from groundwater habitats (mostly wells) and is disjunctly distributed from Butler Co., Kansas, northeastward to Franklin Co., Kansas and Cass Co., Missouri and then southeastward to Camden Co., Missouri. Sexually mature males, 18.0 to 19.5 mm; sexually mature females, 14.5 to 18.0 mm. Ovigerous females are unknown to date and very little is known about the biology of this species.

23. *Stygonectes ozarkensis* Holsinger, 1967
Type Locality: Marvel Cave, Stone Co., Missouri.
This is a somewhat variable species, apparently closely related to *Stygonectes clantoni*, but primarily restricted to cave streams of the southwestern corner of the Ozark Plateau region (southwestern Missouri northwestern Arkansas, and northeastern Oklahoma). Since 1967, this species has been recorded from Tumbling Creek Cave, Taney Co., Smittle Cave, Wright Co., and Fantastic Caverns, Greene Co., Missouri; Cave Springs Cave, Benton Co., Arkansas; and Three Forks Cave, Adair Co., Oklahoma. The Greene and Wright County populations show possible evidence of intergrading with *Stygonectes clantoni* but this needs further study. Sexually mature males, 15.0 to 18.5 mm; sexually mature females, 13.0 to 16.5 mm. Ovigerous females have not been collected and little is known about the biology of this species.

24. *Stygonectes bowmani* Holsinger, 1967
Type Locality: Seep at Girl Scout Camp, 3.2 miles south of Locust Grove, Mayes Co., Oklahoma.
This rather small, poorly known species is based on 8 females and 8 juveniles collected from the type locality. Sexually mature females, 6.0 to 7.0 mm. Male unknown. One of the females in the type series (May collection) was ovigerous.

*Flagellatus* group

25. *Stygonectes flagellatus* (Benedict, 1896)
Type Locality: Artesian well at San Marcos, Hays Co., Texas.
This rare species is known only from the type locality and nearby Ezells Cave. Sexually mature males, 10.5 to 12.0 mm; sexually mature females 7.5 (?) to 14.0 mm. Although collections are available from the months of April, May, June, and October, few specimens have been taken and ovigerous females are still unknown.

26. *Stygonectes longipes* Holsinger, 1966
Type Locality: Cave Without-A-Name (Century Caverns), Kendall Co., Texas.
This species is authentically recorded only from the type locality, although a single, partially broken specimen is known from Bad Weather Pit Cave in nearby Comal County and appears to be conspecific. Sexually mature males, 9.0 to 12.0 (?) mm; sexually mature females, 10.5 to 12.0 mm. A single ovigerous female is known from a collection made in May from a stream in the type locality.

27. *Stygonectes pecki* Holsinger, 1967
Type Locality: Spring in Landa Park (Comal Springs), New Braunfels, Comal Co., Texas.
This rare species is known only from two females, both of which are from the type locality. The larger female (near sexual maturity) = 10.5 mm.

28. *Stygonectes dejectus* Holsinger, 1967
Type Locality: Cascade Cave, Kendall Co., Texas.
This species is known only from two females collected from a pool in the type locality. The larger female = 8.25 mm.

*Hadenoecus* group

29. *Stygonectes hadenoecus* Holsinger, 1966
Type Locality: Devils Sinkhole Cave, Edwards Co., Texas.
This species is known only from its type locality where it is rather common in pools with bat guano and the cirolanid isopod *Cirolanides texensis*. Sexually mature males, 9.0 to 10.0 mm; sexually mature females, 10.0 to 12.0 mm. Although collections have been made during March, June, and October, ovigerous females are still unknown.

## Genus *Stygobromus* Cope, 1872

The subterranean genus *Stygobromus* is widely distributed in the groundwaters of the United States, with species concentrations in the cave regions of the Appalachians, Interior Low plateaus, Ozarks, and far west. As presently defined, the genus contains 10 described and approximately 50 undescribed species in North America and one poorly known species from Siberia. The latter, *S. pusillus* (Martynov, 1930), was described from Telelzkoye Lake in 1930 but recent attempts to locate this material for further study have not been successful, and the status of this species remains vague. A fairly recent redescription of this genus was given by Shoemaker (1942a).

### Key to the North American Species of *Stygobromus*

1 Apical margin of telson entire, not distinctly cleft..... 2
Apical margin of telson distinctly cleft..... 5

2(1) Gnathopodal propod 2 of male greatly enlarged, palmar margin with a distinct notch (Fig. 26a); posterior junction of dactyl and propod of pereopods 6 and 7 with several long, thread-like setae (Fig. 26b); basis of pereopod 7 broad, distoposterior corner subquadrate: *S. heteropodus*
Gnathopodal propod 2 of male not greatly enlarged, palmar margin without a notch; setae at junction of dactyl and propod of pereopods 6 and 7 not elongate or thread-like; basis of pereopod 7 not so broad, distoposterior corner rounded..... 3

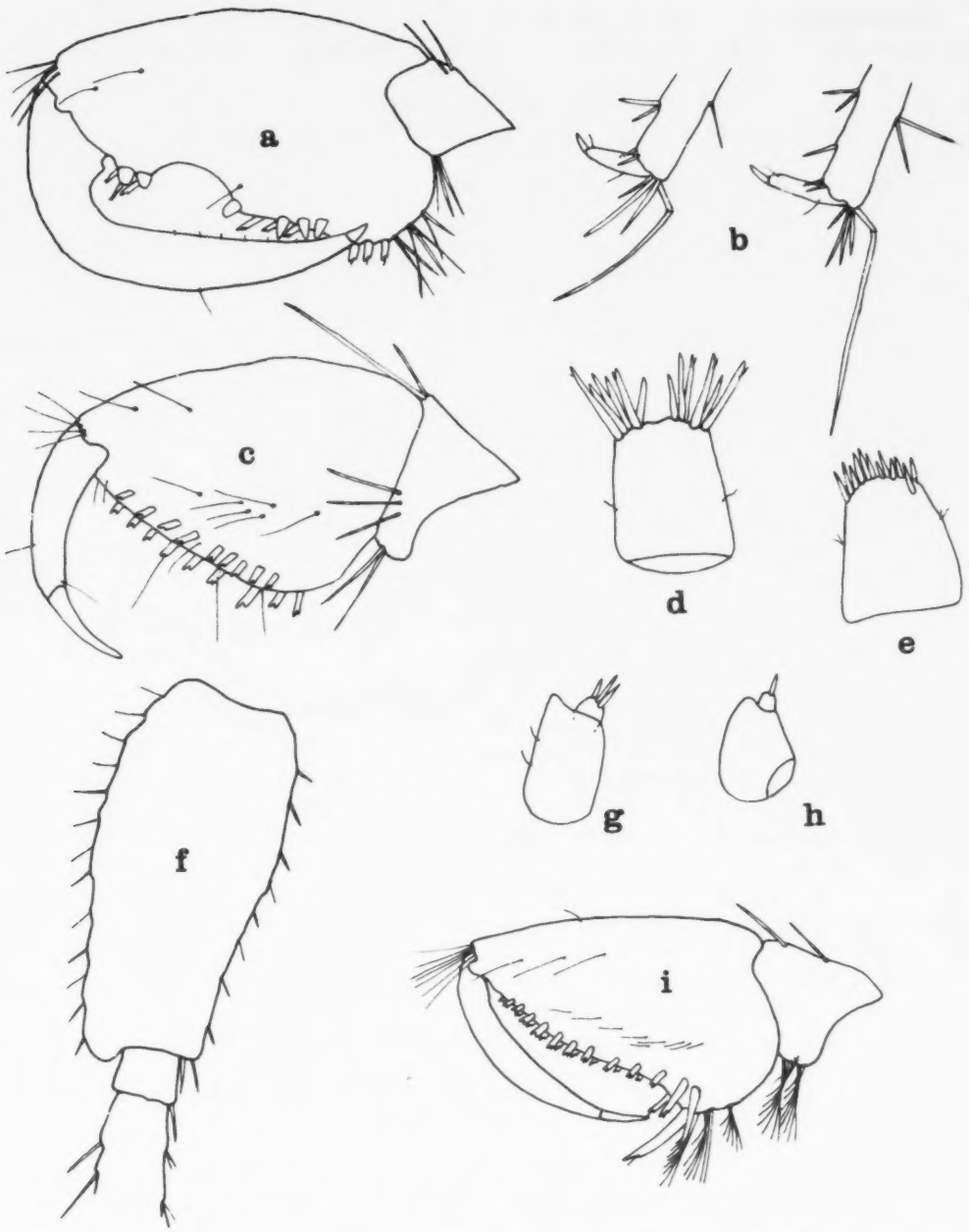


Figure 26. -- Structure of *Stygobromus*: a, 2nd gnathopodal propod of male of *S. heteropodus* (based on Hubricht, 1943); b, dactyls of pereopods 6 and 7 of *S. heteropodus*; c, 1st gnathopodal propod of *S. spinosus* (based on Hubricht and Mackin, 1940); d, telson of *S. exilis*; e, telson of *S. onondagaensis*; f, basis of pereopod 7 of *S. hubbsi* (based on Shoemaker, 1942b); g, uropod 3 of *S. vitreus*; h, uropod 3 of *S. smithi*; i, 2nd gnathopodal propod of *S. smithi* (modified from Hubricht, 1943).

3(2) Pereopods 6 and 7 and gnathopodal propods 1 and 2 about equal in length and size, respectively; posterior margin of gnathopodal propod 1 short, without setae (Fig. 26c): *S. spinosus*

Gnathopodal propod 2 larger than 1; pereopod 6 a little longer than 7; posterior margin of gnathopodal propod 1 lined with a row of setae..... 4

4(3) Palmar margin of female gnathopodal propod 2 oblique, posterior margin about 1/3 as long as propod; dactyls of pereopods 6 and 7 up to 1/3 as long as corresponding propods; telson short and rather broad, armed with 10 to 20 comparatively short apical spines (Fig. 26e): *S. onondagaensis*

Palmar margin of female gnathopodal propod 2 only slightly oblique, posterior margin at least 1/2 as long as propod; dactyls of pereopods 6 and 7 1/3 to 1/2 as long as corresponding propods; telson proportionately longer and more narrow, armed with 10 to 20 comparatively long spines (Fig. 26d): *S. exilis*

5(1) Sternal processes absent..... 6

Sternal processes present..... 7

6(5) Gnathopodal propod 2 long and narrow, palmar margin long and oblique and about 3/4 as long as propod; bases of pereopods 5, 6, and 7 rather long and narrow, posterior margins not expanded (Fig. 26f): *S. hubbsi*

Gnathopodal propod 2 not especially long or narrow, palmar margin oblique but only about 2/3 as long as propod; bases of pereopods 5, 6, and 7 with slightly convex posterior margins: *S. putealis*

7(5) Gnathopodal propod 1 nearly as large as 2, with long, oblique palmar margin continuous with posterior margin; peduncle of uropod 3 with usually 1 prominent spine (sometimes absent in male): *S. mackini*

Gnathopodal propod 1 distinctly smaller than 2, palmar margin not so oblique and forming definite angle (defining angle) at junction with posterior margin; peduncle of uropod 3 without spines (although 1 or 2 stiff setae may be present)..... 8

8(7) Defining angle of gnathopodal propod 2 very distinct (Fig. 26i); outer ramus of uropod 3 tiny and with 1 spine (Fig. 26h); telson with 16 to 20 apical spines: *S. smithi*

Defining angle of gnathopodal propod 2 not very distinct; outer ramus of uropod 3 larger and with 2 to 3 spines (Fig. 26g); telson with 8 to 15 apical spines..... 9

9(8) Gnathopodal propod 2 nearly twice the size of 1; posterior margin of gnathopodal propod 1 with a row of 5 to 10 setae; median sternal and pleonite sternal processes present (the latter occasionally absent in the male): *S. vitreus*

Gnathopodal propod 2 only a little larger than 1; posterior margin of gnathopodal propod 1 nearly devoid of setae; median sternal and pleonite sternal processes absent: *S. iowae*

## Annotated List of the Species

1. *Stygobromus exilis* Hubricht, 1943
Type Locality: Mammoth Onyx Cave, Hart Co., Kentucky.
The range of this predominately cavernicolous species extends from southcentral Kentucky southward through central Tennessee and possibly into Alabama to as far south as Clarke County (Fig. 27). There is considerable variation in this species, however, and the populations from central Tennessee and Alabama may constitute one or two separate (undescribed) species or subspecies. A more accurate delimitation of the range must await further study. *S. exilis* is a common inhabitant of mud-bottom drip and seep pools but is occasionally found in small streams; it is also known from one surface seep in the Mammoth Cave area. This species occurs rarely with *Stygobromus vitreus* (in the Mammoth Cave area) and frequently with *Crangonyx* spp. (often with *Crangonyx packardi*). Sexually mature males, 4.0 to 5.5 mm; sexually mature females, 3.5 to 8.5 mm (but usually 4.5 to 6.5 mm). Newly hatched young = 1.3 to 1.4 mm. Ovigerous females have been observed in spring, summer, and fall and mature specimens the year around. The brood size varies from two to nine eggs depending on the size of the female. Between eight and ten distinct, undescribed species, all of which share morphological affinities with *S. exilis*, occur in caves of the Interior Low Plateau region from northern Alabama to central Kentucky.

2. *Stygobromus heteropodus* Hubricht, 1943
Type Locality: Small spring in the main valley, Pickle Springs, St. Genevieve Co., Missouri.
This rather unique species is known only from its type locality (Fig. 29). Largest male, 7.0 mm; largest female, 6.5 mm. Virtually nothing is known about the biology of this species except that sexual dimorphism is quite pronounced. A closely related species (undescribed) is known from seeps in Edmonson and Grayson counties, Kentucky.

3. *Stygobromus hubbsi* Shoemaker, 1942b
Type Locality: Malheur Cave, Harney Co., Oregon.
This species is presently known only from pools in the back of a lava tube cave (the type locality) (Fig. 29), where it was collected in company with blind, white planarians (*Kenkia rhynchida* Hyman). Largest males, 5.5 mm; largest females, 6.5 mm. It is interesting to note that, in addition to *S. hubbsi*, 11 other species (all undescribed) of *Stygobromus* have been collected from a variety of groundwater habitats (caves, springs, wells, and the depths of a lake) scattered throughout

the far western United States (west of the continental divide). All of these species are morphologically closely related to *S. hubbsi* and will be described in a subsequent paper. Even a twelfth undescribed species has been collected from this region but it is not closely allied morphologically with *S. hubbsi* and apparently belongs to another species group.

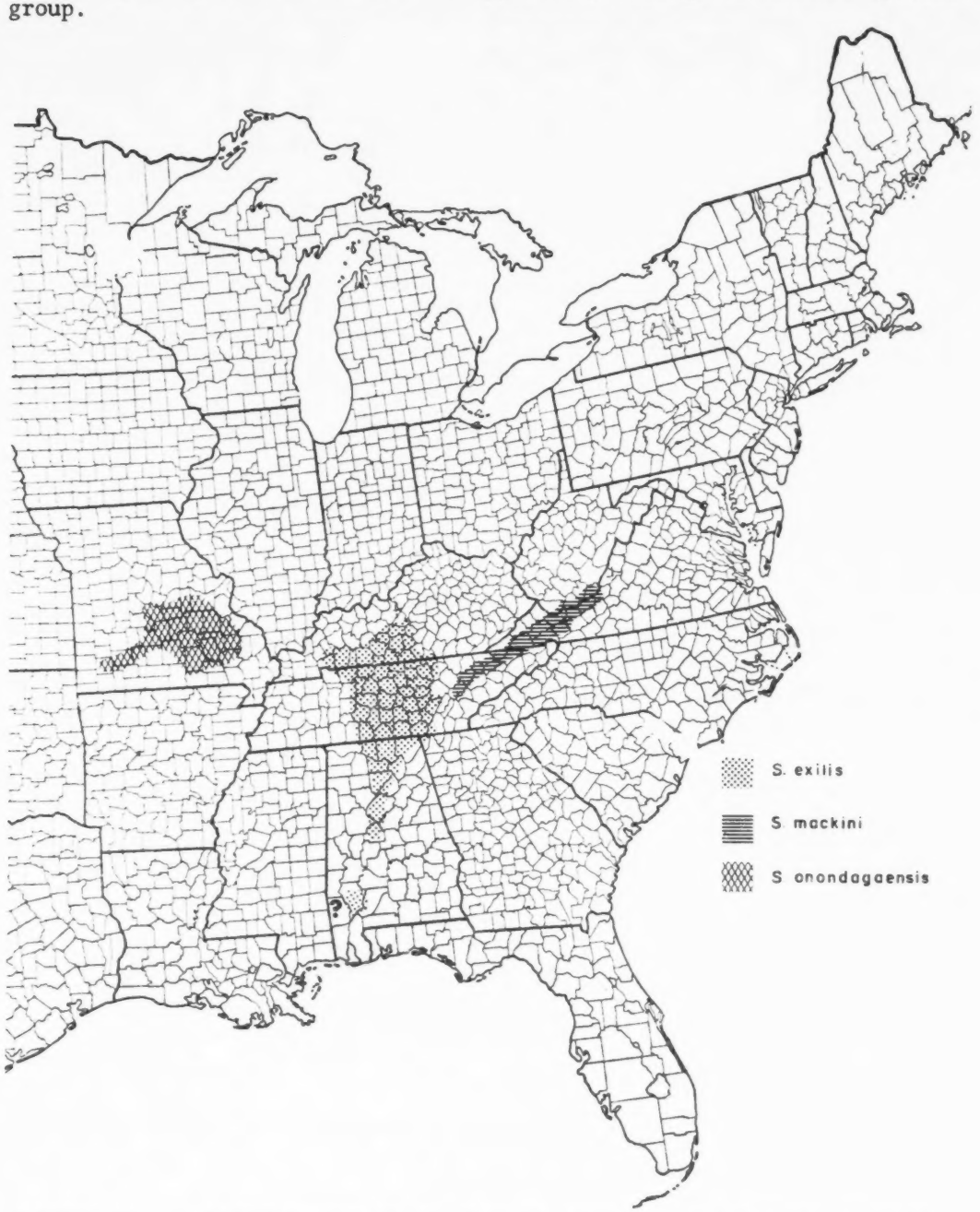


Figure 27. -- Distribution of species of *Stygobromus* in North America.

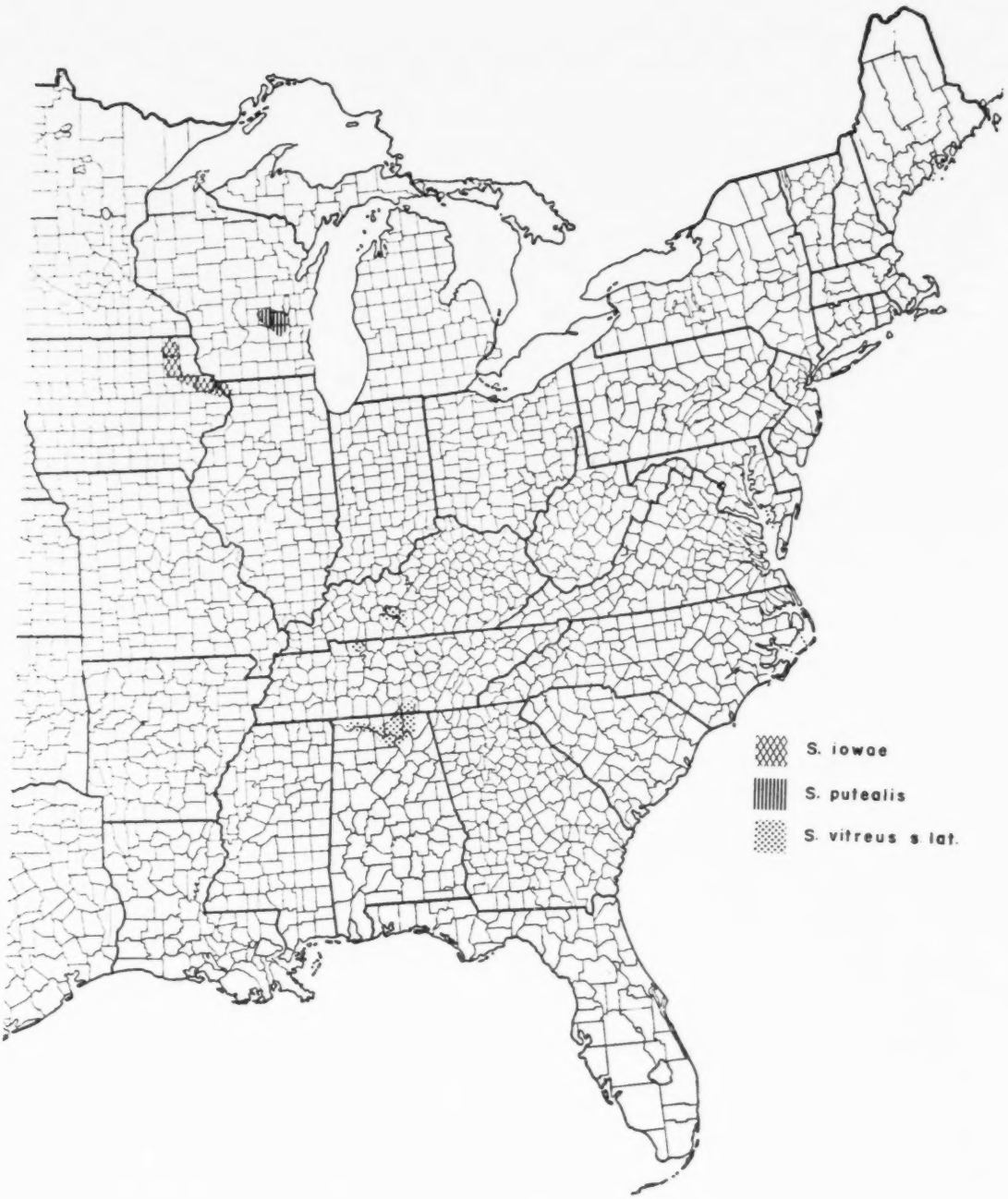


Figure 28. -- Distribution of species of *Stygobromus* in North America.

4. *Stygobromus iowae* Hubricht, 1943
Type Locality: Springs, 0.7 mile north of Fayette, Fayette Co., Iowa.
This subterranean species is presently known from a spring and two caves in northeastern Iowa and from a mine in extreme northwestern Illinois (Fig. 28). Sexually mature males, 5.0 to 5.5 mm; sexually mature females, 4.5 to 6.0 mm. Very little is known about the life cycle except that a single ovigerous female with two embryos was collected from a pool in Skunk Cave, Winneshiek Co., Iowa (July sample).

5. *Stygobromus mackini* Hubricht, 1943
Type Locality: Sikes Cave, Russell Co., Virginia.
The range of this rather common troglobitic species extends from Monroe Co., West Virginia and Craig Co., Virginia south-southwestward through the Appalachian valley to Roane Co., Tennessee (Fig. 27). *S. mackini* is more common in caves in the Clinch River valley (upper Tennessee River drainage) of Tazewell, Russell, and Scott counties, Virginia than anywhere else in its range. This species is commonly found in drip and seep pools (often with mud-bottoms) of caves but one record is from a covered spring in Washington Co., Virginia. Sexually mature males, 5.0 to 7.5 mm; sexually mature females, 4.5 to 10.0 mm. Newly hatched young = approximately 1.7 mm. Ovigerous females brood from four to ten eggs per clutch, depending on the size of the female. Ovigerous females have been observed in spring and summer and mature specimens have been found the year around. A number of undescribed species of *Stygobromus* from caves in northwestern Georgia, northern Alabama and eastern Kentucky are closely related to *S. mackini*, and along with the latter, make up what appears to be a significant species group within the genus.

6. *Stygobromus onondagaensis* (Hubricht and Mackin, 1940)
Type Locality: Onondaga Cave, Crawford Co., Missouri.
This small subterranean species is known primarily from caves in the Ozark region of southcentral Missouri (Fig. 27). The majority of samples (13 out of 20) have come from drip pools in caves, although a few have been taken from small cave streams (four) and surface seeps (three). Sexually mature males, 3.0 to 4.5 mm; sexually mature females, 3.5 to 6.0 mm (but rarely over 5.0 mm). Newly hatched young = approximately 1.5 mm. Ovigerous females have been collected during the summer and fall. In addition to *S. onondagaensis*, at least three undescribed species of the genus occur in the Ozark region and all are apparently closely related to the former.

7. *Stygobromus putealis* (Holmes, 1909)
Type Locality: Well at Waupun, Dodge Co., Wisconsin.
This species is currently known from five wells in three counties in southeastern Wisconsin (Fig. 28). Of some zoogeographic interest is the fact that *S. putealis* appears to be more closely related to species of the *S. hubbsi* group from west of the continental divide than to any of the middle-western species of the genus. Sexually mature males, 3.5 to 3.8 mm; sexually mature females, 4.5 to 6.0 mm. Ovigerous females are not available and samples are too few to determine anything about the biology of this species.

8. *Stygobromus smithi* Hubricht, 1943
Type Locality: S.C. Roden's well, Woodstock, Bibb Co., Alabama.
This rather distinct but apparently rare species is known only foom its type locality and a seep in Tuscaloosa Co., Alabama (Fig. 29). Largest male, 6.0 mm; largest female, 7.5 mm. Nothing is known about the biology of this species.

9. *Stygobromus spinosus* (Hubricht and Mackin, 1940)
Type Locality: Spring near Hawksbill Mountain, Madison Co., Virginia.
This rather unusual blind, white species inhabits small springs and spring runs in the Blue Ridge Mountains of Northern Virginia, and its range extends from Warren County south along the Skyline Drive (Shenandoah National Park) to Augusta County (Fig. 29). *S. spinosus* is often abundant in the gravel substrate of spring runs, under dead leaves, and in masses of aquatic vegetation. Sexually mature males, 4.0 mm; sexually mature females, 3.5 to 5.5 mm. Ovigerous females and sexually mature specimens occur in the spring but only samples from March, May and June have been studied to date. A number of other species, all of which are undescribed, have been collected from caves in the Appalachian valley which lies adjacent to the Blue Ridge Mountains (Holsinger, 1969a). Descriptions of these species are in preparation by the writer.

10. *Stygobromus vitreus* Cope, 1872
Type Locality: Mammoth Cave, Edmonson Co., Kentucky.
This species is found in the Mammoth Cave area of southcentral Kentucky with scattered populations in central Tennessee and northern Alabama (Fig. 28). The Alabama populations differ slightly from those in Kentucky, however, and may be subspecifically (if not specifically!) distinct. *S. vitreus* inhabits small drip and seep pools in caves but is occasionally found in surface seeps in the Mammoth Cave area. Sexually mature males, 4.0 to 6.0 mm; sexually mature females, 3.5 to 7.0 mm. The clutch size of ovigerous females ranges from four to ten eggs, depending on size of the female. Ovigerous females occur in spring, summer, and fall (and probably also in the winter) and mature specimens are found the year around.

Figure 29. -- Distribution of species of *Stygobromus* in North America.

## Genus *Bactrurus* W.P. Hay, 1903

The Genus *Bactrurus* is composed of three described subterranean species which occupy ground water biotopes (mostly seeps, drains, and caves) in the middle-western United States. At least one undescribed species and one undescribed subspecies also occur in this area. The genus is endemic to North America, and while apparently closely related to *Stygonectes*, it is easily distinguished from the latter by the third uropod which has a larger outer ramus and the presence of a rudimentary inner ramus.

### Key to the Species of *Bactrurus*

1. Telson of male very long and cylindrical (Fig. 30a); palmar margins of gnathopodal propods slightly concave; outer ramus of uropod 3 tapering apically, armed with only a few spines (Fig. 5f); sexually mature specimens ranging in size from 8.0 to 15.5 mm: *B. mucronatus*

   Telson normal, not elongate or cylindrical in either sex; palmar margins of gnathopodal propods straight to slightly convex; outer ramus of uropod 3 rounded or blunt apically, armed with 10 to 12 spines (Fig. 30b); size of sexually mature specimens from 13.0 to 28.0 mm..... 2

2(1) Apical margin of telson entire or only slightly notched, armed with rather short spines (Fig. 30c); size range of sexually mature specimens from 15.0 to 28.5 mm: *B. brachycaudus*

   Apical margin of telson distinctly notched, armed with rather long spines (Fig. 30d); size of sexually mature specimens from 13.0 to 21.5 mm: *B. hubrichti*

### Annotated List of the Species

1. *Bactrurus brachycaudus* Hubricht and Mackin, 1940

Type Locality: Walled spring on Keifer Creek, 0.6 mile northwest of Fern Glen, St. Louis Co., Missouri.

This large, subterranean species is found in cave streams, springs, and seeps in southwestern Illinois and eastcentral Missouri (Fig. 31). Sexually mature males reach 27.0 mm; sexually mature females range in size from 15.0 to 28.0 mm, with the average size of ovigerous females being 20.0 mm. Sexually mature specimens occur throughout the year but ovigerous females are rare in samples and so far are known only from collections made in June, August, and September. The largest clutch size observed was 27 eggs in a female, 20.0 mm long (August sample). The presence of mature and immature animals in samples representative of all months of the year probably indicate that at least some reproduction occurs throughout the year. There is, however, a preponderance of juvenile and immature specimens in April samples, thus implying the possibility of a seasonal reproductive peak.

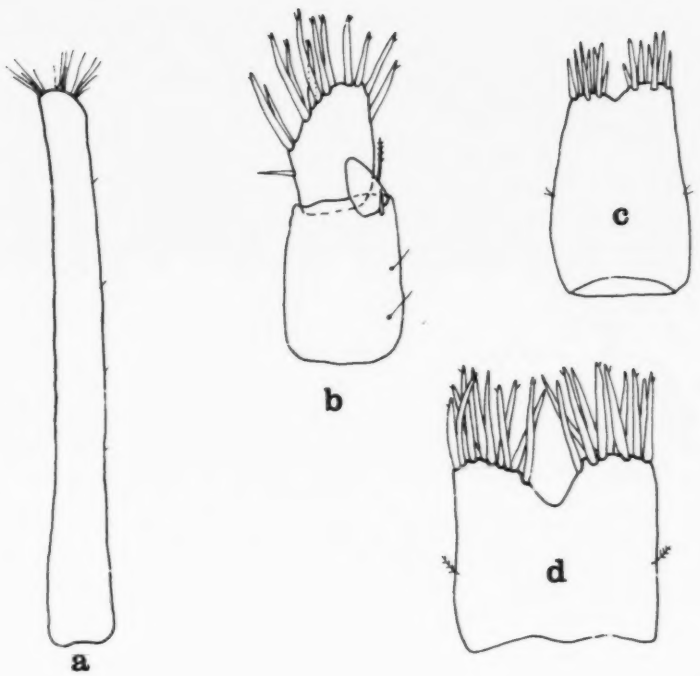


Figure 30. -- Structure of *Bactrurus*: a, telson of male of *B. mucronatus*; b, uropod 3 of *B. hubrichti* (based on Shoemaker, 1945); c, telson of *B. brachycaudus* (based on Hubricht and Mackin, 1940); d, telson of *B. hubrichti* (based on Shoemaker, 1945).

2. *Bactrurus hubrichti* Shoemaker, 1945
Type Locality: Well at Topeka, Shawnee Co., Kansas.
This poorly known species has a spotty distribution, with records from eastern Kansas, eastcentral Oklahoma, and central Missouri (Fig. 31). It is known primarily from wells but is occasionally found in seeps (one in Kansas) and caves (one in Missouri). Sexually mature males, 15.0 to 21.5 mm; sexually mature females, 13.0 to 20.0 mm. Nothing definitive is known of the life cycle except that mature specimens are recorded throughout the year. Ovigerous females are unknown.

3. *Bactrurus mucronatus* (Forbes, 1876)
Type Locality: Well at Normal, McLean Co., Illinois.
This rather common interstitial species is widely distributed from central Ohio north to southern Michigan, across northcentral Indiana and Illinois to southeastern Iowa; it also occurs in caves in Saline County in southeastern Illinois (Fig. 31). This species is common in the outlets of drains in the glaciated areas of the middle-western United States and is occasionally found in wells and caves. Sexually mature males, 9.0 to 15.5 mm; sexually mature females, 8.0 to 14.0 mm. Mature specimens are found in samples taken throughout the year but ovigerous females have not been observed. A closely related species or subspecies occurs in seeps and cave pools in southcentral Missouri and northcentral Arkansas and differs from *B. mucronatus* s. str. in being smaller at sexual maturity and possessing median sternal processes. In this form, sexually mature males are 9.0 to 13.5 mm and sexually mature females are 5.0 to 9.0 mm. Ovigerous females are known from a sample made in May from a seep in Douglas Co., Missouri. These ovigerous females were between 5.0 and 6.0 mm and some had up to 10 eggs per clutch.

Figure 31. -- Distribution of species of *Bactrurus* in North America.

## *Allocrangonyx* Group

### Genus *Allocrangonyx* Schellenberg, 1936

This unique subterranean genus is represented by two species that occupy groundwater habitats in the Arbuckle Mountains of southcentral Oklahoma and the Ozark plateau (Salem plateau section) region of central Missouri. Although this genus shares some morphological affinities with both the European genus *Niphargus* and the predominantly North American genus *Crangonyx*, it also embraces an unusual combination of characters, making it, in the writer's opinion, the single member of a distinct group of the family Gammaridae. The evolutionary affinities and zoogeographic relationships of this genus were discussed in a recent paper by Holsinger (1971).

#### Key to the Species of *Allocrangonyx*

1 Antenna 1 up to 65 percent as long as body in sexually mature animals; pereopod 7 about 55 percent as long as body; dactyls of pereopods 6 and 7 without sets of spines on inner margins; outer ramus of third uropod of sexually mature male with up to 5, rarely 6, secondary segments (Fig. 32b); telson with 6 to 7 apical spines per lobe: *A. pellucidus*

Antenna 1 from 70 to 85 percent as long as body in sexually mature animals; pereopod 7 from 65 to 70 percent as long as body; dactyls of pereopods 6 and 7 with 3 sets of spines on inner margins (Fig. 32a); outer ramus of third uropod of sexually mature male with up to 16 (8-16) secondary segments; telson with 4 apical spines per lobe: *A. hubrichti*

#### Annotated List of the Species

1. *Allocrangonyx pellucidus* (Mackin, 1935)
Type Locality: Bird's Mill Spring, Pontotoc Co., Oklahoma.
This species is known from cave pools, springs, and a seep developed in the Ordovician limestones of the Arbuckle Mountains of southcentral Oklahoma. The range extends from southwestern Murray County northeastward to southern Pontotoc County (see Holsinger, 1971 for a distribution map). Sexually mature males, 22.0 mm; sexually mature females, 18.0 mm. Very little is known about the life cycle except that ovigerous females have been observed in January and February.

2. *Allocrangonyx hubrichti* Holsinger, 1971
Type Locality: Saltpetre Cave, Phelps Co., Missouri.
This species is easily distinguished from *A. pellucidus* by the characters given in the key and its geographic distribution. It is known only from the small streams of two caves in central Missouri (Phelps and Pulaski Counties). Very little data are available on life history, except that a single ovigerous female (14.5) was found in a collection made in October and sexually mature adults were collected from the same cave in August. The writer (Holsinger, 1971) reported a male, 15.0 mm long, with nine secondary segments in the outer ramus of the third uropod.

The third uropod was, in turn, 45 percent as long as the body. Topotypic material, collected since the description of this species, reveals, however, that sexually mature males reach 18.0 mm in length and have up to 16 secondary segments in the outer ramus of the third uropod. The third uropods in larger males are 65 percent as long as the body. Sexually mature females range in size from 14.5 to 17.0 mm.

Figure 32. -- Structure of *Allocrangonyx*: a, dactyls of pereopods 6 and 7 of *A. hubrichti*; b, uropod 3 of mature male of *A. pellucidus*.

## SECTION III

## ACKNOWLEDGMENTS

The writer is grateful to the many persons who have contributed specimens and related information used in the preparation of this manual and to those who have assisted with the field work during the past several years. Credits to individuals contributing specimens and assisting with field work were given in earlier papers or will be given in future ones. Several colleagues, including Dr. J. Laurens Barnard, Dr. E. L. Bousfield, Dr. Thomas E. Bowman, Dr. Gerald A. Cole, Dr. David C. Culver, Mr. Leslie Hubricht, and Dr. Milan Straskraba, offered helpful advice and made useful comments, and their interest is appreciated.

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SECTION IV

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## SECTION V

## GLOSSARY

*Cavernicole.* A species that completes all or at least part of its life cycle in a cave; a cave inhabitant.

*Epigean.* The surface environment as opposed to the subsurface or subterranean environment; the latter is often called *hypogean.*

*Groundwater.* Subsurface or subterranean water, sometimes directly observable in caves and wells or in surface springs and seeps.

*Interstital.* Used in reference to both species and habitats. Interstital species are usually defined as very minute forms (i.e., less than 1 or 2 mm long) that live in the interstices between gravels and sand grains. However, the term is sometimes applied to certain amphipods as long as 10 mm (or rarely, longer) which inhabit cracks and crevices saturated by groundwater.

*Karst.* The surface terrane in an area underlain by carbonate rocks (usually limestone or dolomite), characterized by subsurface drainage sinkholes, caves, bare rock ledges, and large springs.

*Phreatobite.* A species obligatory to subterranean waters but not necessarily restricted to cave habitats (see definition of *troglobite* below).

*Seep.* A place where groundwater flows (seeps) to the surface of the ground. Seeps, in contrast to *springs*, are usually smaller and often temporary or intermittent, depending upon the level of the ground water-table at a given time or place.

*Subterranean.* Used interchangeably with *hypogean* to refer to habitats or species that exist or occur beneath the surface in caves, wells, interstices, etc.

*Syntopic.* Two or more related species that occupy the same macrohabitat. In comparison, *sympatry* refers to an overlap in range but not necessarily in habitat.

*Troglobite.* A species obligatory to caves or related subterranean habitats, usually distinguished morphologically by regression of pigment and photoreceptors and frequently by longer, more attenuated appendages than its epigean congener. Troglobite usually refers more specifically to an obligatory cavernicole, while phreatobite is used in a more general sense for obligatory groundwater species (see definition of *phreatobite*, above).

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